STUDIES OF TROGODERMA SPECIES DEVELOPMENT AND STARVATION, AND EFFECTS OF THEIR HASTISETAE ON SELECTED STORED-PRODUCT INSECTS

by

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INTRODUCTION

Trogoderma variabile Ballion and Trogoderma inclusum LeConte are capable of maintaining populations on a wide range of stored commodities including cereal grains. The larval stage is chiefly responsible for damaging and contaminating the products. When materials are infested by Trogoderma species, numerous larval cast-off skins are often seen in and on the materials. Adults of Trogoderma are quite harmless in terms of damaging the products, for they normally move away from original infestation sites and fly to and feed on flower pollen and nectar. The species are usually found in places such as warehouses, food processing plants, and grain storages where environment is often relatively stable and the conditions are suitable for their continuous development.

Trogoderma larvae possess characteristic setae called hastisetae. Hastisetae are one of the most complex and specialized hairs known among insects (Hinton, 1945). Their function is not completely understood, but previous investigators have shown it to be defensive. They incapacitate other insects by entangling their appendages (Nutting and Spangler, 1969; Mills and Partida, 1976). Trogoderma larvae are also of potential medical importance. They have been associated with digestive upsets, eye irritations, and probably allergies (Okumura, 1967; Mills and Partida, 1976).

It was not known whether or not the adult Trogoderma in the same habitat with their own larvae were affected by the hastisetae. A part of my study was to investigate this question. It also seem appropriate to investigate the attachment mechanisms of the hastisetae in relation to external morphology and behavior of selected stored-product insects when exposed to Trogoderma

larvae. Relative susceptibility of the selected stored-product insects to the hastisetae and the probable causes of differences in susceptibility were determined.

I also examined the possibility of competition between Trogoderma variabile and each of two other stored-product insects in the same habitat.

An interesting characteristic of Trogoderma larvae is their ability to survive long periods without food, which is important for their survival in emptied warehouses, granaries, etc. However, few authors have reported the effects of starvation on Trogoderma larvae and no reports were found on starvation of T. variabile, therefore a part of my study was to evaluate the effects of starvation of T. variabile and T. inclusum larvae and to record observations of changes in certain characteristics.

I also evaluated certain developmental characteristics of fed T. variabile larvae in comparison with the starved larvae.

LITERATURE REVIEW

Economic Importance

Trogoderma parabile was first described by Beal (1954) as a new Nearctic species. Mroczkowski (1968) reported the name as a synonym for a European species T. variabile Ballion. Beal (1954) mentioned that T. parabile (T. variabile) appeared to have potential for economic significance. Strong, et al (1959) listed the hosts or possible host materials of T. variabile from survey reports and stated that 77 materials had been identified as being associated with infestations of this species. They included cereal grains, seeds, dried fruits, nuts, animal feeds (plant origin), grocery commodities, fish meal, and chicken manure. Strong et al. (1959) successfully reared T. variabile on ground barley, ground corn, ground wheat, ground dogfood and poultry laying mash in a laboratory. The species occurs throughout the United States but seems to be prevalent in the drier areas (Beal, 1960).

Trogoderma inclusum has not been found in as many host materials as T. variabile. Strong et al. (1959) listed 33 materials that were found infested by the species, including cereal grains, seeds, animal feeds, and grocery commodities. Beal (1956) stated that although T. inclusum is often found in grain storage, it had not been established that it can subsist on grain alone. It is a common pest in dried milk and is often found infesting a wide range of other dried protein substances. Strong (1975) examined the host range of this species by exposing the insects to various commodities and determined the multiplication capabilities. He stated that T. inclusum is more likely to be an industrial pest,

infesting dried foods and animal feeds in processing plants and storage facilities, than a serious pest of stored grain.

In the Stored-Product Insects Laboratory at Kansas State University, both T. inclusum and T. variabile have been successfully maintained for several years on poultry laying mash with some dog biscuits on the top.

Biological and Behavioral Aspects

Partida and Strong (1975) studied T. variabile as part of a series of biological investigations of Trogoderma species. They found that the eggs took 6 days for hatching, and 32.1 and 36.6 days were required for males and females, respectively, to develop from hatching to mature adults under favorable conditions of 32.2°C, 50% RH. They stated that females did not require multiple matings to lay all of their eggs. They evaluated suitability of 26 selected foods and the results showed high multiplication on rolled oats, rolled barley, dogfood, and oatmeal. Life history and behavior of T. variabile, under the name of T. parabile, was investigated by Loschiavo (1960). Under 32°C and 70% RH constant conditions, the mean adult life span was 14.3 days and the mean life cycle, oviposition to adult emergence, was 43.2 (range 39-50) days.

Strong (1975) studied the biology of T. inclusum under laboratory conditions. At optimum temperature of 32.2°C with 50% RH, egg incubation period was 5.2 days, and from egg hatching to mature adult required 36.8 days for males and 41.7 days for females. Male and female larvae molted 5 and 6 times, respectively.

Pupation and adult maturation periods were 4.8 days for males and 4.7 days for females. Oviposition lasted an average of 6.8 days. An average of 84.8 larvae were produced from eggs laid by each fecund female. Thirty-two representative foods were tested for rearing the insects. Pollen was the most preferred, followed by mixed animal feeds (poultry laying mash, dogfoods, etc.), processed grains, and several grocery commodities.

Hadaway (1956) discussed the ability of larval Trogoderma to remain on rough surfaces of some materials, due to numerous hairs on their bodies. He stated that the hairs enabled the larvae to cling to sacks or clothing of workmen, and thus be transported.

Nutting and Spangler (1969) observed defensive or threatening behavior of T. variabile larvae against several species of insects and some vertebrates. In response to a stimulus, such as contact by an intruding insect, the larva waved its last several abdominal segments in a circular motion, or toward the source of the stimulus; many hastisetae were pulled off from the larvae and became attached to the intruder. There seemed to be no differences in larval response to various kinds of stimuli. T. variabile larvae responded not only to intruding insects, such as ants and hemipteran predators, but also reacted to pungent vapors, e.g. organic acids, alcohol, and propionic anhydride in a similar way.

Mills and Partida (1976) demonstrated the mechanisms of attachment of the hastisetae against 4 species of stored-product insects by using a scanning electron microscope (SEM). They also stated that the hastisetae and the larval behavior probably serve to defend them against certain small predators and parasites.

Ma et al. (1978) reported that the larvae of Anthrenus flavipes possess a bundle of caudal spicisetae on a special structure called the "supra-anal organ" on the last abdominal segment; the organ vibrates the spicisetae when the larva moves. They stated that the supra-anal organ with the spicisetae serves to defend the larva from potential predators or parasites.

There have been a few studies of competition between Trogoderma species and other stored-product insects. Bains and Atwal (1972) studied the populations of the two major insects of stored grains in India and found that conditions for successful multiplication of Trogoderma granarium Everts and Sitophilus oryzae (L.), an internal feeder, appeared to be quite different. The rate of increase of T. granarium was very low when temperature and grain moisture were most favorable for multiplication of S. oryzae. When conditions were such that high populations of T. granarium developed, S. oryzae populations did not survive. Bains et al. (1977) stated that the two species often infest the same mass of grain and their ultimate populations are the net result of interspecific competition under variable conditions of temperature and humidity. They stated that the initial grain temperature, the capacity of the competing species to modify it and the relative intrinsic rate of increase at a particular temperature were the important factors influencing the outcome of competition.

Yinon and Shulov (1969) conducted a laboratory study of a substance of adult T. granarium that seems to act as a repellent against Tribolium castaneum. They observed that the substance was more abundant in females than males. The fact that T. castaneum preyed on specimens of T. granarium

only when the latter species were dead, at which time the active substance had evaporated from their bodies, suggested the possibility that the substance had a defensive role. It did not appear to be specific, i.e. acting only against Tribolium species, nor a conventional sex-attractant.

Starvation Resistance

Trogoderma larvae are known to survive extremely long periods without food. Riley (1883) reported one T. tarsale (T. inclusum) larva still alive after 3.5 years of confinement in a metal box. Wodsedalek (1917) conducted an experiment using T. tarsale (T. inclusum) larvae of varying size and stated that the largest larvae (about 8 mm) dwindled to the hatching length of 1 mm after 4 to 4.5 years of starvation. This species is not known to eat their cast skins. Khare (1965) determined the 'median death' (day corresponding to the 6th death of a 10-larval cohort) of isolated starved larvae of 3 stored-product insects. He found that T. granarium larvae could resist starvation for 279 days, whereas T. castaneum larvae lasted 28 days, and R. dominica larvae for 17 days. T. granarium larvae decreased in size during starvation, and the color of the larvae diminished from brown to light brown, and ultimately to yellowish brown.

Beck (1971a, b; 1972; 1973a, b) conducted extensive studies on growth and retrogression of Trogoderma glabrum larvae. When deprived of food, they underwent partially reversed development, "retrogressive" larval molts occurred, and the larvae diminished in size and weight. Given foods, the larvae molted and regained their previous degree of maturity. Repeated cycles of retrogression and "regrowth" were possible.

Beck and Bharadwaj (1972) also found that the fat body cells of retrogressed T. glabrum larvae were highly polyploid, indicating physiological deterioration, i.e. aging.

Scanning Electron Microscopy

Mills and Partida (1976) revealed the attachment mechanisms of the hastisetae, whereby they bound or entangled the appendages of other insects. Elbert (1976) examined and compared the hastisetae within the subfamily Anthreninae using both scanning and transmission electron microscopes. Structural variations of the hastisetae among the species of the subfamily were shown. Most recently, Kvenberg (1978) presented scanning electron micrographs of elytra of numerous stored-product beetles, including Trogoderma, for use in insect fragment identification in commodities. In Family Dermestidae, setae modification is evident in the genus Anthrenus; the broad fan-shaped scales bearing a number of ribs or pleats are characteristic of the genus. He stated that there is a marked similarity of circular, concave setal pits in all common species of Dermestidae.

GENERAL MATERIALS AND METHODS

Only general materials and methods are included in this sections. Detailed methods and materials pertinent to each of the experimental tests are described in each section.

Insects

Both T. variabile and T. inclusum were collected in Kansas and have been cultured in the Stored-Product Insects Laboratory, Department of Entomology, for several years. Identifications were confirmed by Lloyd Knutson, USDA, Science and Education Administration, Agricultural Research, on October 20, 1978.

Maintenance of Cultures

A growth chamber (Percival) was used to rear the insects. The temperature and relative humidity were monitored by a hygrothermograph (Belfort Instrument Company). The temperature was constant; 27 $\pm$ 1°C (80 $\pm$ 1°F), and relative humidity averaged 43%, varying between 12 to 68%. The extreme relative humidities were of short duration. A saturated potassium carbonate solution in a large tray was placed in the chamber to assist in regulation of the relative humidity. A 16:8, light:dark, photoperiod was maintained in the chamber.

Pint jars or quart jars were used for rearing the insects. The jars were closed on top by using brass screen, and Kelthane-treated filter papers were inserted in the metal closure rings. The treated filter papers

were to protect cultures from mite infestation. The culture medium was composed of 95% of poultry laying mash (All Purpose Mash, Farmer's Cooperative Association) and 5% of dry yeast (Active Dry Yeast for Bakers, Fleischmann's) by volume. Each jar was filled 1/3-full when the culture was started and fresh food was added occasionally. A few pieces of dog biscuits (Milk Bone, Nabisco Inc.) were placed on top of the medium for additional food. Small, immature larvae preferred to feed on them making holes in them. Three pieces of corrugated cardboard (4.0 x 6.0 cm) were placed on top of the dog biscuits as refuges for the larvae. Generally, the large, mature larvae aggregated on the lower surface of the pieces of the cardboard or crawled into the corrugated grooves. When cast skins accumulated to about 1 cm deep on top of each culture jar, the top layer of medium (without cast skins) was transferred to fresh medium in a new culture jar. The old cultures were then destroyed.

Scanning Electron Microscopy

A scanning electron microscope (ETEC U-1) was used for detailed morphological studies. Specimens were first mounted on aluminum stubs (1.3 cm diam.) with either double adhesive tape (Double-Coated Scotch Tape) or with clear fingernail polish, depending on the insects. They were coated with gold-palladium under vacuum. Magnifications ranged from about 10x to 6000x and 2.5, 5, or 10 kv's were used for accelerating voltage.

EXPERIMENTAL TESTS

I. Susceptibility of Trogoderma variabile and T. inclusum Adults to Hastisetae of Their Larvae.

Description of Hastisetae

Three types of setae or hairs are on the Trogoderma larval body. They are; nudisetae, spicisetae, and hastisetae. Nudisetae are straight and simple hairs, commonly found on coleopterous larvae. Spicisetae are short to long hairs coming out from sockets and with overlapping sharply-pointed scales. The longest spicisetae are located at the last abdominal segment and extend longitudinally. Earlier instars tend to have a higher ratio between length of the spicisetae and body length, i.e. younger larvae have longer "tails", or caudal brushes, in relation to their body lengths as compared with the older or mature larvae. The function of both nudisetae and spicisetae are believed to be sensory.

Hinton (1945) developed a key to dermestid larvae and differentiated subfamily Anthreninae into 2 groups according to characteristics of the hastisetae: (1) conspicuous tufts of the hastisetae are on the 5th, 6th, and 7th abdominal tergites in Anthrenus species, (2) the tufts are on the 5th, 6th, 7th, and 8th abdominal tergites of the rest of the genera including Trogoderma species. Elbert (1976) examined the morphological characteristics of the hastisetae among Anthreninae by using transmission and scanning electron microscopes and compared the hastisetae of each species.

The hastisetae have very complex structure with an arrowhead shaped head (Plate I, Fig. 1) and long shaft with "rosettes" along the length.

The structure of the hastisetae is shown in Plate I, Fig. 2, together with some spicisetae (indicated by arrows). The interior structure of a hastisetal head was revealed in a partially broken hastiseta (Plate I, Fig. 3). The head portion of a hastiseta has 6 lobes and there appears to be a cap-like structure at the tip of the head (Plate I, Fig. 4). The hastisetae on Trogoderma larvae are found on all parts of the dorsal surface of the larval body from prothoracic to the 8th abdominal segments postero-laterally; however, they are rather sparse except for pairs of dense tufts on the 5th, 6th, 7th, and 8th abdominal segments of a full-grown larva (Plate II, Fig. 1). The tufts with abundant hastisetae (on 5th to 8th abdominal tergites) will be referred to here as "major" hastisetal tufts. A lateral view of a full-grown larva of T. variabile is shown in Plate II, Fig. 2. A major hastisetal tuft and spicisetae are shown in Plate II, Fig. 3. The hastisetae are found even on newly-hatched first instar larva (Plate II, Fig. 4). The number of hastisetae in a tuft and the number of hastisetal tufts increase as the larva develops, and the full-grown larva has 4 pairs of major hastisetal tufts. Okumura (1967) reported that 1600 to 3000 hastisetae were found on a mature Trogoderma variabile larva.

The hastisetae are easily detached from the larvae leaving short "stubs" on the body surface (Plate III, Fig. 1). Furthermore, after they are pulled off they may interlock with each other forming chains and a mass (Plate III, Fig. 2). Setae of other insects may wedge in the slots of the rosettes along the stem, or in the slots of the hastisetal head. An example is shown in Plate III, Fig. 3. This particular hastisetal

EXPLANATION OF PLATE I

Trogoderma inclusion hastisetae (marker line = 10 μ)

Fig. 1: Head portion of a hastiseta.

Fig. 2: Sparsely distributed hastisetae. Spicisetae and their sockets are indicated by arrows.

Trogoderma variabile hastisetae

Fig. 3: Partially broken hastiseta attached to a lesser grain borer, showing interior structure of the hastisetal head (marker line = 10 μ).

Fig. 4: Hastisetal head with its 6 lobes as seen from the tip (marker line = 1 μ).

PLATE I

Fig. 1

Fig. 2

Fig. 3

Fig. 4

EXPLANATION OF PLATE II

Trogoderma variabile larva (marker lines = 100 μ)

Fig. 1: Full-grown larva; dorsal view.

Fig. 2: Full-grown larva; lateral view of the last several abdominal segments. Arrows indicate the "major" hastisetal tufts.

Fig. 3: Major hastisetal tuft.

Fig. 4: First instar larva has only a few hastisetae on 7th and 8th abdominal tergites.

PLATE II

Fig. 1

Fig. 2

Fig. 3

Fig. 4

EXPLANATION OF PLATE III

The mechanisms of the hastisetae; their detachment, interlocking, and attachment to other insect's setae.

Fig. 1: Several hastisetae were detached leaving stubs, indicated by arrows. Some apparently came out from their sockets (Photo from studies by Mills and Partida, 1976).

Fig. 2: The stem of one hastiseta wedged between the lobes of the head of another hastiseta (Photo from Mills and Partida, 1976).

Fig. 3: Setae of a drugstore beetle caught in slots of the head of a hastiseta, indicated by arrows. (marker line = 10 μ).

Fig. 4: A seta on a cigarette beetle antenna wedged in a slot of a "rosette" on the stem of a hastiseta (marker line = 10 μ).

PLATE III

Fig. 1

Fig. 2

Fig. 3

Fig. 4

head was found on a drugstore beetle leg; many setae from the beetle were tightly wedged in the slots of the head. Rosettes are also capable of tightly holding other insects' setae and appendages. Plate III, Fig. 4 shows a seta of a cigarette beetle's antenna wedged in the slot of a rosette.

When Trogoderma larvae are touched or disturbed by other insects, they wiggle their posterior ends (last few abdominal segments) in a circular motion as if trying to defend themselves by exposing the hastisetal tufts against the intruder.

Many hastisetae are easily pulled off and may entangle the appendages of the intruder. Thus the hastisetae apparently are a defense mechanism of Trogoderma larvae.

Effects of Hastisetae on Trogoderma Adults

The mechanism of how adult Trogoderma can protect themselves from the potentially dangerous defensive behavior of the larvae against encountered insects has not been reported. Experiments were conducted to determine how adult Trogoderma avoid being entangled by the larval hastisetae.

Materials and Methods

Male and female T. variabile and T. inclusum (age-unknown) were randomly selected from cultures and kept separate. Sexes were determined by antennal characteristics and also body size of the insects. For each species, 5 males or 5 females were introduced into a clean, small plastic

box (15 x 20 x 20 mm) with 3 mature larvae of the same species. For each species, 5 males or females were placed in another box without the larvae, as controls. Three replications and three controls were made for each species. Behavior of the adults in each box was carefully observed for 2-3 min. under a binocular dissecting microscope at 30-min. intervals for 2 hr. No physical disturbance was used to force contact between the adults and the larvae. After 2 hr, each box was shaken for 1 min., then observations were continued for another 3 hr. After 5 hr of observation, all insects were put into a freezer to quickly inactivate them, and kill them to maintain the attachment of the larval hastisetae on the adults. The adults were mounted on stubs for detailed study using the scanning electron microscope (SEM).

In the second test, male and female pupae of T. inclusum were selected from cultures and sexed according to size. A glass petri dish (9 cm diam.) with a small amount of food was used to hold pupae of each sex until adult emergence. Emerged adults were aspirated from the dishes daily for 5 days, their sexes were confirmed by observing antennal characteristics, and transferred to another dish for each sex. No food was supplied in the second dish, but small pieces of water-soaked tissue papers were placed in it. On the 6th day, 5 male and 5 female adults (age: 1-6 days) were taken from the petri dishes and introduced into 2 plastic boxes, sexes separate. Three full-grown larvae of T. inclusum were added to each box. Three replications and 3 controls (5 adults in each box without Trogoderma larvae) were set up for each sex. The boxes were not disturbed, except when carefully handled for observations under a binocular dissecting microscope (x 10.5 to x 45). Observations were made at exposures of 12,

24, 48, and 72 hr. Both normal and abnormal adult behavior was recorded. The sites of hastisetal attachment on the adults were observed under the binocular microscope and the number of hastisetae attached to them were estimated. The number of adults alive was also recorded at each observation.

Results and Discussion

None of the adult beetles died throughout the experiment in either test. In control boxes, there was no unusual behavior of the beetles. During the observations, some of the adults were found climbing the walls of the boxes as if trying to escape, and some remained quiet at the bottom of the boxes, both in test and in control boxes. The behavioral responses of the two Trogoderma species observed in the first test were similar and are summarized below.

After a short period of restless movements, all of the beetles, especially females, tended to aggregate quietly in corners of the boxes, 2-3/corner. This was observed through the first 2 hr. No such behavior was observed for the larvae. They tended to move around, trying to climb the walls of the box and did not aggregate. When at rest, both male and female adults retracted their antennae into the antennal cavities (Plate IV, Fig. 1). Males have deeper antennal cavities than females (Plate V, Fig. 1,2,3,4), probably for protection of their longer antennae. The same characteristics were apparent for T. inclusum (Plate VI, Fig. 1,2). As the beetles walk, they raise their heads and their antennae are extended forward. But when touched by another beetle or by a larva, the antennae were retracted into the cavities. During the first 2 hr of the test,

EXPLANATION OF PLATE IV

Trogoderma variabile adults.

Fig. 1: Female, left; male, right, has longer antennae than female (marker line = 100 μ).

Fig. 2: Female with attached hastisetae, especially on exposed tip of hind-wing and on antennae (marker line = 100 μ).

Fig. 1

Fig. 2

EXPLANATION OF PLATE V

Trogoderma variabile adults (marker line = 100 μ)

Fig. 1: Male with antenna retracted into cavity.

Fig. 2: Male antenna and cavity.

Fig. 3: Female.

Fig. 4: Female antennal cavity is shallower than male's.

PLATE V

Fig. 1

Fig. 2

Fig. 3

Fig. 4

EXPLANATION OF PLATE VI

Trogoderma inclusum adults (marker line = 100 μ).

Fig. 1: Male with longer antennae than female

Fig. 2: Female.

PLATE VI

Fig. 1

Fig. 2

adult beetles picked up a few hastisetae on their appendages, but there was no severe entanglement of the appendages. Males picked up more hastisetae on their antennae than females.

Shaking the beetles and the larvae together in the boxes after the first 2 hr observation resulted in more hastisetae becoming attached to the adults and they began active "cleaning behavior". Forelegs were effectively used to rid antennae of the hastisetae, and mouthparts were used to pull off or chew off the hastisetae attached to the forelegs and antennae. Middle and hind legs were also used to remove the hastisetae from the abdomen and these accumulated as a ball, or wad, at the tip of the abdomen. Protruding and retracting the abdomen also accumulated hastisetae at the tip. Occasionally, rather extensive attachment occurred on some appendages, restricting normal movement of the beetles (Plate IV, Fig. 2), but there seemed to be relatively fewer hastisetae attached to elytra, abdomen, and thorax. Hastisetae on legs were usually easily cleaned off, while antennae were more susceptible to hastisetae which seemed more difficult to remove. The structure of the adult beetles most vulnerable to hastisetae were the hindwings. This was demonstrated by artificially removing one elytron from a female T. inclusum adult (Plate VII, Fig. 1,2, 3,4). It was possible for the adult to clean the hastisetae from antennae and legs, but the hastisetae on the hindwings appeared to be permanently attached to the setae of the wings. When hastisetae attached to hindwings were numerous, the beetles could not fold back their elytra to the normal position. Sometimes 2 individuals were bound together by hastisetae attached to their hindwings.

EXPLANATION OF PLATE VII

Trogoderma inclusum (♀); one elytron was removed, then the insect was exposed to a mass of hastisetae. Arrows indicate one hastisetal attachment site.

Fig. 1: Numerous hastisetae attached to the insect. Arrow points to one hastisetal attachment, magnified in following figures (marker line = 100 μ).

Fig. 2: Hindwing and abdominal segments with hastisetae attached (marker line = 100 μ).

Fig. 3: Head of hastisetae attached to seta on hindwing (marker line = 10 μ).

Fig. 4: Same as Fig. 3, further enlarged (marker line = 10 μ).

PLATE VII

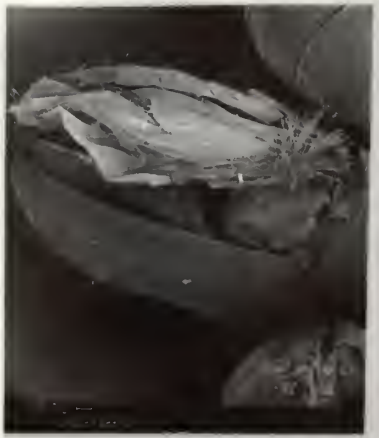


Fig. 1

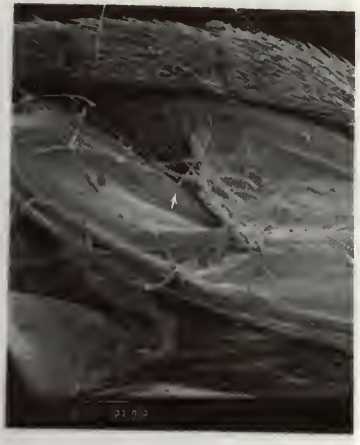


Fig. 2

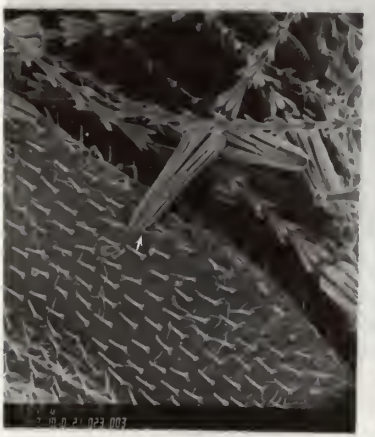


Fig. 3

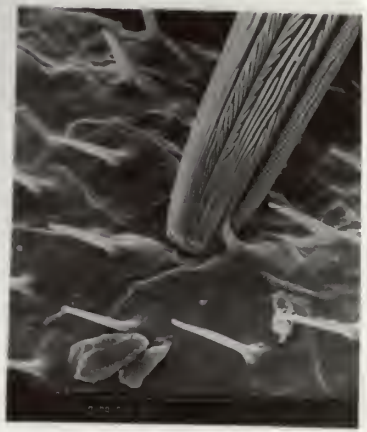


Fig. 4

In the second test, T. inclusum adults and larvae were intentionally undisturbed throughout an experiment lasting for 72 hr, i.e. they were not forced into contact with each other. Observations made during the test were as follows:

After 12 hr, there was little movement; the beetles were resting quietly on the bottom of the box. Usually 1 or 2 hastisetae were attached to the antennae of each male and female in boxes with the larvae. Aggregation of both males and females was more apparent for controls than for test insects.

After 24 hr, the abdomens usually had more hastisetae on them than did the elytra. Hastisetae on legs were more easily rubbed off during cleaning behavior than those on or around the head (antennae, mouthparts, and frons area).

After 48 hr, at least 2 to 3 hastisetae were found on antennae of most of the test beetles, both males and females. One male had a hastiseta attached to the eye, but it was eventually cleaned off.

After 72 hr, about 3 to 5 broken-off spicisetae per insect were on the bodies of most of the adult test beetles, but they did not appear to be attached, and were easily removed by the insects.

It seems that Trogoderma adults have innate mechanisms to protect themselves from the potentially dangerous hastisetae of their own larvae. One factor is the structure of the setae on the adult body. As seen in SEM photos (Plate VIII, Fig. 1), setae on elytra are so thick in diameter that they apparently cannot wedge in the slots of the heads of the hastisetae. The setae decrease in diameter and length, in order, from elytra to legs (Plate VIII, Fig. 2), antennae (Plate VIII, Fig. 3), and

EXPLANATION OF PLATE VIII

Various sizes and densities of Trogoderma inclusum adult setae. Magnification, 3500 x (marker line = 10 μ).

Fig. 1: Setae on elytra; sparsely distributed and relatively large setae on body.

Fig. 2: Setae on leg (tibia).

Fig. 3: Setae on antenna; the density is the greatest among the sites observed, but setae are smaller than those on elytra and legs.

Fig. 4: Setae on hindwing; the density is less than on the antennae and the size is smaller.

PLATE VIII

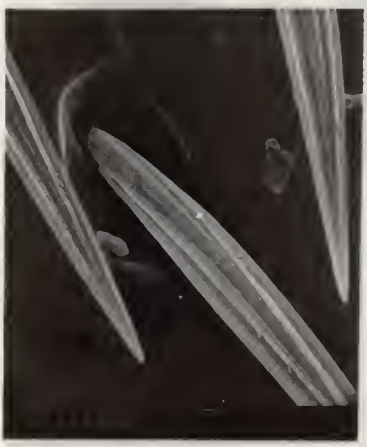


Fig. 1

Fig. 2

Fig. 3

Fig. 4

to hindwings (Plate VIII, Fig. 4). Magnification was the same (3500x) on all of the SEM photos in Plate VIII. The most vulnerable part of the adult body to the hastisetae were the hindwings. The setae on the hindwings are small enough in diameter to be caught by the heads or rosettes of the hastisetae.

Another factor is the length of the adult antennae. Males of T. variabile and T. inclusum have longer antennae than females and thus would be expected to be more vulnerable to hastisetae. But males have deeper antennal cavities than females and this no doubt furnishes better protection as shown in Plate V. When ready to pupate, mature larvae either crawl into cracks and crevices or move up to the surface of the medium. If a layer of cast-off skins is present on the medium, the larvae move up onto it and pupate. Trogoderma pupate within the last larval skin, probably for protection. After adult eclosion, the insect stays within the last larval skin until it matures. Pupation on top of the medium ensures that adults would have less exposure to hastisetae, either on the larvae or loose in the medium. If pupation were to take place in the medium or within the layer of cast skins, newly-emerged adults would be exposed to many hastisetae as they move to the surface. The behavior of the adult staying in the last larval skin until maturation reduces the exposure to the larval hastisetae, especially when the adult is young and has a soft cuticle.

II. Relative Susceptibility of Selected Stored-Product Insects to the Effects of Trogoderma Hastisetae.

Experiments were conducted to evaluate the relative susceptibility of the adults of 11 species of stored-product insects to Trogoderma larval hastisetae. Larvae of two species were also tested. Some of these species are possible competitors for the same kind of food with Trogoderma species. Comparative morphological studies especially of setae, were made using the SEM, and species reactions to the hastisetae were also observed.

Materials and Methods

The adults of the species listed below were taken from active cultures maintained in a rearing room (27 ± 1°C; 67 ± 3% RH; 14:10hr, light:dark).

Species	Rearing medium
Rice weevil; Sitophilus oryzae (L.)	hard red winter wheat (Eagle variety)
Lesser grain borer; Rhyzopertha dominica (Fabricius)	same as above
Red flour beetle; Tribolium castaneum (Herbst)	63 parts of whole wheat flour, 32 parts of corn meal, and 5 parts of dry yeast
Confused flour beetle; T. confusum Jacquelin duVal	same as above
Flat grain beetle; Cryptolestes pusillus (Schonherr)	95 parts of rolled oats, 5 parts of dry yeast
Foreign grain beetle; Ahasverus advena (Waltl)	same as above

Sawtoothed grain beetle; Oryzaephilus surinamensis (L.)	same as flat grain beetle
Drugstore beetle; Stegobium paniceum (L.)	same as the flour beetles except some dogfood was added on the top (Milk Bone, Nabisco Inc.)
Cigarette beetle; Lasioderma serricorne (F.)	same as above
Shiny spider beetle; Gibbium psylloides (Czenpinski)	same as above
Cadelle; Tenebroides mauritanicus (L.)	mixed medium of poultry laying mash, corn kernels

Five adults of each species were introduced into a plastic box as used in Experimental Test I. No sexing was performed except for the flat grain beetle, where 3 males and 3 females were put into each box. Sexes were determined on the basis of the longer antennae of the males. All adults used in this experiment were of unknown age (7 to 30 days). Three mature larvae of either T. variabile or T. inclusum were added to each box. Three replications and 3 controls (Trogoderma larvae excluded) were tested. After 12, 24, 48, and 72 hr, careful observations using a binocular microscope were made of the behavior of the test adults and of the attachment sites of hastisetae. The number of hastisetae on various sites of the beetles' bodies was also estimated. Number of insects found dead was recorded at each observation. After 72 hr, all insects were transferred to a freezer for killing to preserve the entanglement situations. Specimens of these stored-product insects were then used for SEM study.

Results and Discussion

Insects in control boxes apparently tried to escape by climbing up the walls when first introduced, but this behavior generally subsided after 12 hr. They were either walking normally or resting quietly throughout the rest of the experimental period. Some insects were observed to copulate in the boxes. Only two rice weevils, 1 cadelle and 1 male flat grain beetle died in the control boxes during the 72 hr. Mortality ranged from 0 to 100% in the test boxes (Table 1). Except in one of the replicates of the foreign grain beetle where all 5 insects were entangled and dead at the 24 hr observation, no mortality was recorded at the 12 or 24 hr observations. Therefore the mortality results are shown only for the 48 and 72 hr observations. Reactions of a particular species to Trogoderma larvae were similar in all replicates, thus the mortalities were pooled to obtain the mean percent mortality. Significant increases in mortality were recorded at the 48 and 72 hr observations for the rice weevil and flat grain beetle. The highest mortality was observed for rice weevils exposed to T. variabile larvae (53.3% at 48 hr, and 100% at 72 hr); there was no significant difference in mortality for the weevils exposed to either T. variabile or T. inclusum larvae. Flat grain beetles exhibited the second highest mortality, averaging 50.0% at the 48 hr and 83.3% at the 72 hr observations when the insects were exposed to T. variabile larvae. There were no differences in mortality between T. variabile-exposed and T. inclusum-exposed flat grain beetles. In both cases, 94.4% of the males and 72.2% of the females were entangled and dead at the final observation. Longer antennae probably made the males more susceptible than females,

Table 1. Percent mortalities of stored-product insects exposed to Trogoderma larvae.

SPI[1] species	Life[2] stage	T.[3] species	% mortality[4] 48 hr	% mortality[4] 72 hr
Rice weevil	A	T. var.	46.7cde	93.3ab
"	"	T. incl.	53.3cd	100.0a
Flat grain beetle	"	T. var.	50.0cde	83.3ab
"	"	T. incl.	44.4cde	83.3ab
"	L	T. var.	20.0de	26.7de
Foreign grain beetle	A	T. var.	33.3cde	73.3bc
Drugstore beetle	"	T. var.	0.0e	40.0de
Sawtoothed grain beetle	"	T. var.	0.0e	13.3de
"	"	T. incl.	26.7de	40.0cde
Lesser grain borer	"	T. var.	0.0e	26.7de
Cigarette beetle	"	T. var.	0.0e	20.0de
Shiny spider beetle	"	T. var.	0.0e	6.7de
Red flour beetle	"	T. var.	0.0e	0.0e
"	"	T. incl.	0.0e	6.7de
Confused flour beetle	"	T. var.	0.0e	0.0e
"	L	T. var.	0.0e	0.0e
Cadelle	A	T. var.	0.0e	0.0e

1/ SPI: Stored-product insects.

2/ Life stage: A stands for adult insects, L for larvae that were exposed to Trogoderma larvae.

3/ Trogoderma variabile or T. inclusum.

4/ Means followed by the same letter are not significantly different at the 5% level (Duncan's multiple range test). All data were transformed to arcsin values in order to minimize the large variability.

because the longer antennae are more vulnerable to hastisetal attachment and entanglement. The antennae and legs of susceptible insects, such as flat grain beetles, became hopelessly entangled and the insects eventually died. For the shiny spider beetle and the red flour beetle (exposed to T. inclusum), only one insect of 15 of each case (6.7%) died during the experiment. No mortality was recorded for the cadelle, the confused flour beetle, or the red flour beetle (exposed to T. variabile).

Although detailed observations were recorded, only generalized or more significant observations are listed below. Generally there appeared to be little difference between susceptibility to, or reaction to, hastisetae of the two Trogoderma species, T. variabile and T. inclusum, thus the three replications involving each species are treated together, and reference to hastisetae makes no distinction between the two species.

Flat grain beetles

12 hours

(1) Antennae of most insects were bound together and attached to the legs or other parts of the body by 5-10 hastisetae which had been pulled from the Trogoderma larvae.

(2) Mandibles had been used to cut some hastisetae.

(3) Longer antennae of the males were more vulnerable to hastisetal attachment and binding.

(4) Some body setae to which hastisetae were attached were pulled off as the beetles struggled to remove the hastisetae.

(5) SEM photographs (Plate IX, Figs. 2,3, and 4) show the secure wedging of an antennal setae into the slot of the head of a hastiseta.

EXPLANATION OF PLATE IX

Flat grain beetles entangled by Trogoderma variabile hastisetae.

Fig. 1: Antennae are bound together by hastisetae. Longer male antennae are more vulnerable to hastisetae than female's (marker line = 100 μ).

Fig. 2: Several antennal segments with hastisetae attached. The holes indicate that numerous setae were pulled off, probably while the beetles struggled to free themselves (marker line = 10 μ).

Fig. 3: Arrows indicate hastisetal attachments to setae, in Fig. 2, 3, and 4. Fig. 2 was taken from a different angle than the other two (marker line = 10 μ).

Fig. 4: Secure wedging of the antennal setae into the slots of the hastisetal head is evident. The seta on the right was pulled from its socket (marker line = 10 μ).

PLATE IX

Fig. 1

Fig. 2

Fig. 3

Fig. 4

24 hours

(1) In some boxes (replicates), males were bound to each other by hastisetae attached to their antennae.

(2) Most females were free and moving around in the boxes; a few were bound to the other insects by the hastisetae.

48 hours

(1) Females were also involved in the entangled mass.

(2) Antennae and legs of both sexes were bound together strongly in the groups of entangled insects (Plate IX, Fig. 1).

72 hours

(1) An average of 83.3% of the insects used in the test were dead. The insects still alive each had 10 to 15 hastisetae on abdomen and elytra together.

(2) No mortality was recorded in the controls.

Red flour beetle and confused flour beetle

The observations of red flour beetles and confused flour beetles exposed to Trogoderma variabile and T. inclusum larvae were similar. Therefore the following record and discussion do not distinguish between them.

12 hours

(1) Estimated average number of hastisetae on each insect's elytra was 5-10.

(2) No entanglement of appendages was found, although the total numbers of hastisetae found on their bodies were higher than observed on flat grain beetles.

(3) In each box, a ball of hastisetae about the size of an eye of a flour beetle was attached to parts of the beetles' bodies,

such as legs and elytra. It did not remain attached to one particular beetle in a box all the time, but rather it occasionally transferred from one insect to another.

24 hours

(1) The hastisetal balls, formed due to the extensive cleaning behavior of the beetles using all legs and the mouthparts, increased in size to about the size of the beetle's thorax.

(2) About 10-20 hastisetae were found on each beetle's abdomen and elytra.

48 hours

(1) The hastisetal ball in each box was readily picked up by any beetle that touched it.

72 hours

(1) The size of the hastisetal balls became as large as the beetle's head and thorax combined. The shape of the balls were either spherical or triangular and were so well 'matted' or compacted that fecal materials and miscellaneous particles were trapped in them.

(2) No appendages were found 'curled' or bound together by hastisetae throughout the test.

(3) Some hastisetae were attached to elytra and abdomen as shown in Plate XI, Fig. 1 and 2, but they were readily cleaned off by the legs or became incorporated into the hastisetal ball.

EXPLANATION OF PLATE X

Flat grain beetle; legs and elytra with hastisetae attached.

Fig. 1: Hastisetae attached to leg (marker line = 10 μ).

Fig. 2: Same as Fig. 1, enlarged (marker line = 10 μ).

Fig. 3: Numerous thin setae on the elytra, and two attached hastisetae. (marker line = 10 μ).

Fig. 4: Higher magnification of one of the attachment sites in Fig. 3 (marker line = 10 μ).

PLATE X

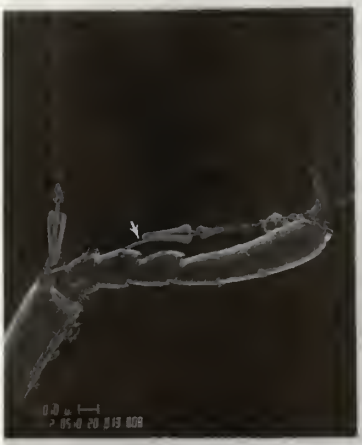


Fig. 1

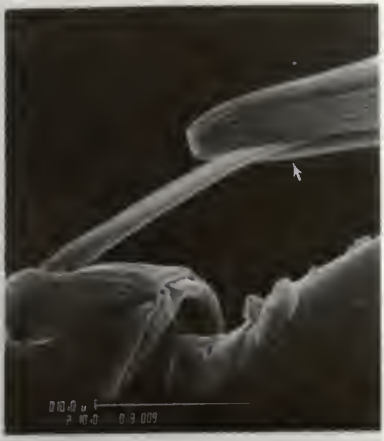


Fig. 2

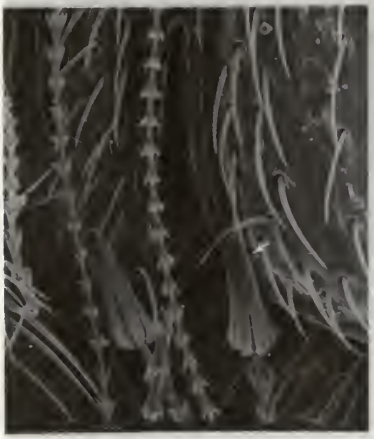


Fig. 3

Fig. 4

EXPLANATION OF PLATE XI

Flour beetles (Tribolium castaneum)

Fig. 1: Hastisetae attached to a red flour beetle elytron. Fewer and shorter setae were found on the body compared with the flat grain beetle in Plate X, Fig. 3 (marker line = 10 μ).

Fig. 2: Smooth appearance of the red flour beetle's ventral side, legs and abdomen, due to low setal density (marker line = 100 μ).

PLATE XI

Fig. 1

Fig. 2

(4) Plate XII, Figs. 1-3 show an example of hastisetal attachment found on a red flour beetle antenna.

(5) Many heads of hastisetae were found attached to the mouthparts of the beetles especially around the labrum area (Plate XII, Fig. 4). This suggested that the beetles tried to clean the hastisetae from their appendages (antennae and forelegs by cutting with the mandibles and the hastisetal heads readily attached to the setae around the mouthparts.

(6) No mortality was recorded in controls throughout the test.

Rice weevil

12 hours

(1) Almost all weevils were found rather tightly entangled with each other, usually 2-5 insects in a group (Plate XIII, Fig. 1).

(2) Each weevil in the group had 10-20 hastisetae on the dorsal and 20-40 on the ventral surface of the body.

(3) In some boxes, a ball containing an estimated 100 hastisetae was found in the middle of the entanglement.

(4) Occasionally some weevils could free themselves and walk away from the mass.

24 hours

(1) Usually, about 7 hastisetae per leg were found on each weevil, but still no hastisetal attachment was observed on antennae.

EXPLANATION OF PLATE XII

Hastisetal attachment on red flour beetles.

Fig. 1,2, & 3: Red flour beetle head. Arrows indicate the same hastisetal attachment site on antenna (marker lines = 100, 10, and 10 μ respectively).

Fig. 4: Hastisetal heads, apparently chewed or chopped by the mandibles (arrow), were attached to the labrum area (marker line = 10 μ).

PLATE XII

Fig. 1

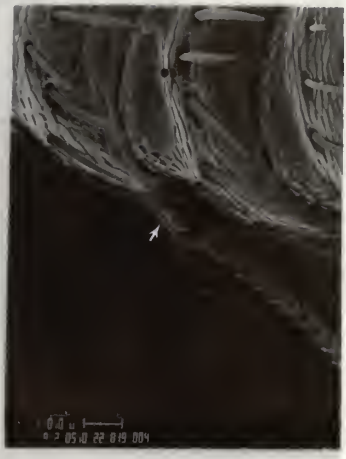


Fig. 2

Fig. 3

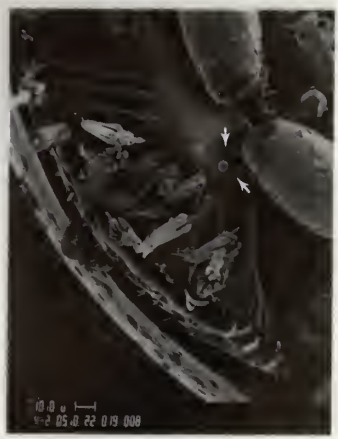


Fig. 4

EXPLANATION OF PLATE XIII

Rice weevil entanglement by hastisetae.

Fig. 1: A group of entangled rice weevils with numerous hastisetae on their bodies, especially on legs (marker line = 100 μ).

Fig. 2: Branches of a compound seta on the leg wedged into a slot of the hastisetal head (marker line = 10 μ).

Fig. 3: A typical compound seta on the elytra; finely branched like a "shrub" blown by wind (marker line = 10 μ).

PLATE XIII

Fig. 1

Fig. 2

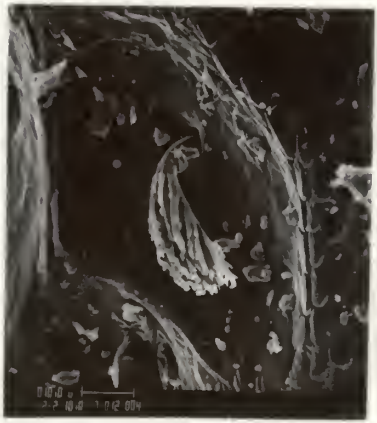


Fig. 3

48 hours

(1) Hastisetal balls were 'irregular-shaped' and not well compacted, as compared to the ones made by the flour beetles.

(2) In entangled groups of insects, 50% (range 20-60%) were dead.

72 hours

(1) Most of the weevils were involved in entangled masses. There was usually one mass consisting of 4-5 insects in each box. In the entangled masses, 73.3% (20-100) were dead.

(2) Although the antennae had relatively fewer hastisetae on them, Plate XIV, Fig. 1-4 illustrates hastisetal attachment found on a weevil's antenna.

(3) Setae on the rice weevil body were branched. Plate XIII, Fig. 2 illustrates a seta on a rice weevil leg strongly wedged in the hastisetal head and a typical seta on the elytra is shown in Plate XIII, Fig. 3.

(4) No mortality was recorded in controls.

Foreign grain beetle (SEM photographs were not taken)

12 hours

(1) Some beetles were entangled legs to legs by interlocking hastisetae.

(2) Hastisetae on antennae were well chewed-up by the insect's mouthparts.

(3) In one box, all the beetles were entangled together by 30-50 hastisetae.

EXPLANATION OF PLATE XIV

Rice weevils: continued.

Fig. 1: Long "snout" (mouthparts at the tip) and elbowed antenna. (Arrows indicate the same hastisetal attachment site. (marker line = 100 μ).

Fig. 2: Two hastisetae attached to the antenna. The tip of the antenna has a different kind of setae (marker line = 10 μ).

Fig. 3 & 4: The seta on the antenna is strongly wedged into the slot of hastisetal head (marker lines = 10 μ).

PLATE XIV

Fig. 1

Fig. 2

Fig. 3

Fig. 4

24 hours

(1) Most of the beetles were entangled in groups of 2-5.

48 hours

(1) Most of the insects in each box were involved in the entanglement.

(2) Average mortality was 33.3% (range 0.0 - 100.0%).

72 hours

(1) Mortality averaged 73.3% (range 40.0 - 100.0%).

(2) Antennae and legs were vulnerable to hastisetal attachment and were usually bound together.

(3) No mortality was recorded in controls.

Drugstore beetle

12 hours

(1) Each beetle had already picked up from 5-10 hastisetae on the head area, and 5-25 on the elytra.

(2) The insects showed characteristic posture. When motionless, the head was held beneath the thorax, and the antennae were retracted underneath the head and thorax. The insects showed the same posture when touched by the Trogoderma larvae (Plate XV, Fig. 1).

24 hours

(1) Legs and antennae were entangled by 10-20 and 5-10 hastisetae, respectively.

(2) Active cleaning behavior using all legs and mouthparts was always observed in insects exposed to the larvae.

EXPLANATION OF PLATE XV

Drugstore beetle and cigarette beetle entanglement by the hastisetae.

Fig. 1: Masses of hastisetae on drugstore beetles. Left arrow indicate the insect head; right, prothorax (marker line = 100 μ).

Fig. 2: "Rosettes" on stem of hastiseta. The arrow indicates a seta on a drugstore beetle's antenna wedged into a slot of a rosette. (marker line = 10 μ).

Fig. 3: Cigarette beetles covered by the hastisetae (marker line = 100 μ).

PLATE XV

Fig. 1

Fig. 2

Fig. 3

48 hours

(1) Usually, entangled beetles could separate themselves after struggling.

(2) The insects in the boxes were getting weak as they were having more trouble climbing up the walls of the boxes than they did at the beginning of the test.

72 hours

(1) Forty percent of the beetles (range 0.0 - 60%) were dead either alone or entangled together.

(2) There were 25 - 30 hastisetae on the abdomen, and 10 - 40 on the elytra of each insect.

(3) No mortality was recorded in controls.

(4) "Rosettes" along the shaft of the hastisetae are also able to catch or hold other insects' setae. Plate XV, Fig. 2 illustrates a seta on a drugstore beetle antenna caught by the rosette.

Cigarette beetles

(1) Only some of the insects were observed using mouthparts to cut off hastisetae attached to antennae and forelegs.

(2) Most insects, though 5 - 15 hastisetae were attached to their bodies, remained quiet instead of struggling to get rid of the hastisetae on their bodies.

(3) While quiet, the insect head was held beneath the prothorax; a characteristic posture of the species (Plate XV, Fig. 3).

24 hours

(1) In all test replicates, all adult insects were involved in hastisetal entanglement.

(2) Each insect had 5 - 15 hastisetae on its abdomen, 10 - 20 on elytra, and usually about 5 on the head.

(3) Relatively small numbers of hastisetae were found binding together an entangled mass of insects, which could not free themselves.

48 hours

(1) Most of the beetles did not actively try to clean or free themselves. They continued to show the characteristic "quiet" posture.

(2) Five to 10 hastisetae were observed on the thorax and 15 - 20 on the elytra of each insect.

(3) There was no mortality.

72 hours

(1) Mortality averaged 20% (range 0.0 - 40.0%) at the final observation.

(2) Although the insects had either picked up hastisetae on their appendages or were involved in entanglement, most of them did not show active cleaning behavior. They generally remained quiet.

(3) Similar posture was observed in control insects (head was held underneath the thorax). There was no mortality in controls.

Lesser grain borer

12 hours

(1) Most of the adult insects were already entangled in groups of 2 - 5 individuals per mass.

(2) A small ball of hastisetae was usually found in each box. The ball was not as compact and round as those made by flour beetles.

24 hours

(1) All adult test insects were bound together as a single mass in each box.

(2) Fifteen to 20 hastisetae were found on the elytra, 15 - 20 on the pronotum, and 3 - 10 on each leg of each insect.

(3) At least one hastisetal ball was found attached to one of the insects in each box, and occasionally it was transferred to another insect (Plate XVI, Fig. 1).

48 hours

(1) Hastisetal balls increased in size in each box, due to additional hastisetae collected during movement and cleaning behavior of the insects.

(2) Legs have relatively few hairs (Plate XVI, Fig. 2) and the cleaning behavior with legs was relatively effective.

(3) Almost no hastisetae were attached to the head, except around the mouthparts as seen in Plate XVI, Fig. 3. The head is usually retracted under the prothorax which forms a 'hood'.

(4) There was no mortality.

EXPLANATION OF PLATE XVI

Lesser grain borer entanglement by the hastisetae.

Fig. 1: The insects made a hastisetal 'ball' (arrow) during cleaning behavior (marker line = 100 μ).

Fig. 2: Seta of leg wedged in hastisetal head. The setal density on legs is relatively low (marker line = 10 μ).

Fig. 3: Due to sparseness and shortness of setae, the head (except around eyes and mouthparts) appears so smooth that hastisetae do not attach (marker line = 100 μ).

PLATE XVII

Fig. 1

Fig. 2

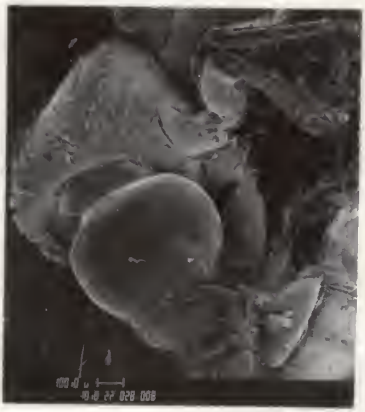


Fig. 3

72 hours

(1) In the entangled masses involving all adult insects, 26.7% (range 0.0 - 40.0%) were dead.

(2) Live insects were using mouthparts to cut off the hastisetae on their appendages.

(3) The pronotum of the insect has numerous spines or tubercles which collected more hastisetae compared with the rest of the body, while the head, which is often retracted into the prothorax, did not collect hastisetae at all, perhaps also because of its smoothness.

(4) No mortality was recorded for the control insects.

Sawtoothed grain beetle

12 hours

(1) Many of the beetles (50 - 60%) were involved in entangled masses consisting of 2 - 3 insects per mass (Plate XVII, Fig. 1).

(2) Some insects had 5 - 10 hastisetae on each antenna, causing "curling" of the antenna. Curling is referred to as a loop of an antenna connected by the hastisetae.

(3) Antennae seemed to be the most vulnerable part of the body. Hastisetae on elytra seemed not to affect the beetles' movement; although if touched by other insects' appendages, they were picked up and attached to the latter insect. Cleaning behavior using mouthparts and all legs was active.

EXPLANATION OF PLATE XVII

Sawtoothed grain beetle entanglement by the hastisetae.

Fig. 1: Antennae and legs of 5 adults are bound together with hastisetae. (marker line = 100 μ).

Fig. 2: Setae on elytra are thick and apparently only the tips will wedge in hastisetal slots (marker line = 10 μ).

Fig. 1

Fig. 2

48 hours

(1) Fewer insects were found entangled in groups than at 24 hr, probably as a result of continuous cleaning effort.

(2) Many fragments of hastisetae were found attached to legs and antennae, perhaps because of the cutting or chewing by the insects.

(3) Mortality averaged 13.3% (range 0.0 - 60.0%).

72 hours

(1) Final average mortality was 23.3% (range 0.0 - 80.0%).

(2) When an insect was found dead, it usually was ventral side up with all legs bound together, and with the antennae curled.

(3) Live insects showed normal movement, except for occasionally using mouthparts for cleaning.

(4) No mortality was observed for the controls.

(5) Setae on elytra are very thick and deeply grooved as shown in Plate XVII, Fig. 2. Usually the beetles struggled more to rid themselves of the hastisetae attached to antennae and legs, rather than hastisetae on elytra.

Shiny spider beetle

12 hours

(1) Most of the beetles were involved in entanglement consisting of 2 - 4 insects per group. They were bound together legs to legs or antennae to legs, by 3 - 5 hastisetae on each leg and 3 - 4 on each antenna.

(2) The insects were occasionally able to free themselves and crawled away from the mass.

24 hours

(1) Each entangled mass involved 2 - 5 insects. Some beetles could free themselves.

(2) Very few hastisetae (less than 5) were found on the elytra of each beetle. These hastisetae were readily removed when another insect touched them.

(3) The beetles spent much of their time with their ventral side up, trying to re-orient themselves and rid themselves of hastisetae at the same time (Plate XVIII, Fig. 1).

(4) The insect is naturally slow-moving, and often "flips" over on its back, then tries to re-orient itself. This is commonly observed in cultures also.

48 hours

(1) Each leg had 5 - 15 hastisetae, and the antennae of some insects were bound in a curl by 5 - 10 hastisetae.

72 hours

(1) Only one beetle died in the test (6.7%). The appendages of the dead insect were severely entangled by hastisetae.

(2) The shape, size, and density of the setae on the legs and the antennae were quite different from the ones on elytra.

EXPLANATION OF PLATE XVIII

Shiny spider beetle.

Fig. 1: Smooth elytra with almost no hastisetal attachment (marker line = 100 μ).

Fig. 2: Susceptible "feather-like" setae on the antennae with hastisetae attached (arrow) (marker line = 10 μ).

Fig. 3: Smooth elytron with few hastisetae (marker line = 100 μ).

Fig. 4: Simple and short seta on elytron (marker line = 10 μ).

PLATE XVIII

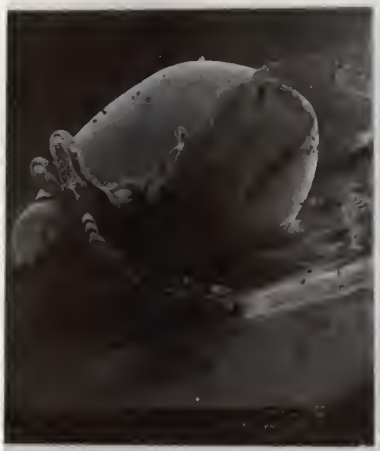


Fig. 1

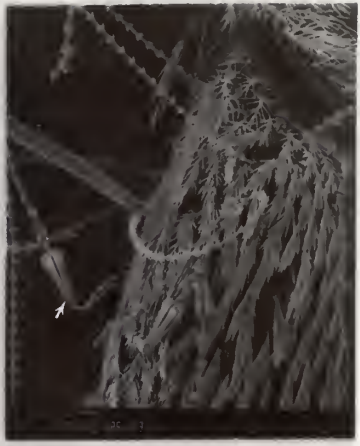


Fig. 2

Fig. 3

Fig. 4

(3) The setae on the antennae with hastisetae attached are shown in Plate XVIII, Fig. 2. These setae were feather-like. They were quite vulnerable to hastisetal attachment. The density of the setae was greater compared with those on elytra.

(4) The elytra were very smooth and shiny (Plate XVIII, Figs. 3 and 4) and with only a few hastisetae attached to them.

(5) In controls, the beetles also tended to "flip" over and cluster, although no Trogoderma larvae were present. No mortality was recorded.

Cadelle

Cadelles were aggressive toward tactile stimuli. If touched, the beetle oriented itself toward the source, opened its strong mandibles and tried to bite. Because of this behavior, introduction of more than one beetle in each box resulted in fighting and biting off of each other's appendages. Thus only one cadelle and 3 Trogoderma larvae were placed in a box (3 replications and 3 controls).

12 hours

(1) Each insect had 5 - 10 hastisetae on each leg, 15 - 35 on the abdomen, 5 - 10 on the elytra, and 5 - 10 on each antenna. The numbers attached were greater than for any other species observed, perhaps influenced by the insect's large size and ability to continue moving and contacting the Trogoderma larvae.

24 hours

(1) The beetles efficiently cleaned the hastisetae from antennae and legs making hastisetal balls between the legs, at the tip of the abdomen, or around the mouthparts (Plate XIX, Fig. 1).

(2) One control insect died. The cause was not apparent.

48 hours

(1) The hastisetal balls on their appendages and on the body surface increased in size. Each beetle had a hastisetal ball at the mouthparts about the size of the insect's eye. The balls were relatively well compacted and the hastisetae in them were chewed and cut by the mouthparts.

(2) One Trogoderma larva was killed by a beetle. It was cut into two at the abdomen and was still held in the beetle's mouthparts (Plate XIX, Fig. 1).

72 hours

(1) There was no further mortality in test insects and only the one control beetle died between 12 and 24 hours of the test.

Booklice

Because of an insufficient number of the insects, the test using booklice was modified. The species was not confirmed, but belonged to the family Liposcelidae. Five booklice were put into a box with 3 Trogoderma larvae. The test was not replicated.

EXPLANATION OF PLATE XIX

Fig. 1: Cadelle with hastisetal balls (arrows) resulting from cleaning activities. At the anterior is a Trogoderma larva cut in two by the cadelle (marker line = 100 μ).

Fig. 2: Entangled booklice: although these booklice were entangled by hastisetae lying loose in the box, they did not appear to be vulnerable to hastisetae still on Trogoderma larvae. Even when they climbed on Trogoderma larvae, they did not pull off hastisetae, perhaps because of their light weight. (marker line = 100 μ).

PLATE XIX

Fig. 1

Fig. 2

(1) Most of the booklice picked up the hastisetae lying loose on the bottom of the box and became hopelessly entangled and died within 24 hr (Plate XIX, Fig. 2).

(2) In another test, booklice occasionally climbed up on the body of the Trogoderma larva, but did not appear to pull hastisetae from the larva; perhaps because they were not heavy enough to pull off the hastisetae.

Flat grain beetle larvae

12 hours

(1) Two of the 5 flat grain beetle larvae in each box were entangled or bound together with 10 - 25 hastisetae between them.

(2) The rest of the larvae in the boxes each had 2 - 10 hastisetae on its body. The head appeared to be the most susceptible to hastisetal attachment.

24 hours

(1) In one replicate, 2 of the flat grain beetle larvae were dead and dessicated. A mass of hastisetae was found in between the entangled larvae.

(2) Some larvae were bound together; head to head, or head to tail with 10 - 30 hastisetae.

48 hours

(1) One larva had a ball of hastisetae (50 - 60 hastisetae) attached to the side of its body, and was dead (3 larvae out of 15 dead).

(2) In the control, one larva died.

72 hours

(1) Average mortality was 26.7% (range 0.0 - 60.0%) at the final observation.

(2) Hastisetae or hastisetal balls were usually attached to the flat grain beetle larval head or to the sides of their bodies.

(3) Some dead larvae were apparently consumed by Trogoderma larvae, for no carcasses of the larvae were found in the box.

Confused flour beetle larvae

12 hours

(1) Hastisetae (20 - 30) were attached to each insect's body, especially on the head and tip of the abdomen.

(2) Occasionally 2 - 3 larvae were stuck together side by side or head to tail, but after a few minutes' struggle, they could free themselves.

24 hours

(1) The head area, especially mouthparts, had many hastisetae (10 - 20) attached.

(2) No serious entanglement between larvae was observed.

48 hours

(1) More hastisetae were found on each larval body (50 - 60), but they did not seem to restrict movement.

72 hours

(1) There was no mortality in tests or in controls.

(2) Sixty to 100 hastisetae were found on each larval body.

(3) Some larvae were bound together in groups of 3 - 4. They were struggling to escape from these entanglements.

Mortalities of the flat grain beetle larvae exposed to Trogoderma larvae were 13.3, 20.0, and 26.7% after 24, 48, and 72 hours, respectively. No larvae of the confused flour beetle died throughout the test.

In summary, it is obvious that the hastisetae of Trogoderma larvae had critical or fatal effect on some of the stored-product species tested. The exposure of the insects confined for 3 days with Trogoderma larvae resulted in various levels of mortality. The species exposed were categorized as susceptible, intermediate, or resistant to the hastisetae, according to percent mortality. The susceptible species were defined as those with more than 60% mortality after 72 hr exposure, and resistant species as having less than 10% mortality. Intermediate species were those in-between. Three species were susceptible: flat grain beetle, foreign grain beetle, and rice weevil. Four species were intermediate: drugstore beetle, lesser grain borer, sawtoothed grain beetle, and cigarette beetle. Confused flour beetle, red flour beetle, shiny spider beetle, and cadelle were resistant.

The 3-day observation period was arbitrarily chosen, and with longer exposure periods, the results may have been different; probably with higher mortality and perhaps a change in the ranking of the species with regard to susceptibility. However, the results of the tests indicated that the percent mortalities were significantly higher among the insects exposed to Trogoderma larvae than among the unexposed control insects, except in resistant species where almost no insects died either in tests or controls.

There seems to be two factors involved in the responses of stored-product insects against Trogoderma hastisetae. They are behavioral and morphological. An example of behavioral differences that resulted in different mortality levels was the drugstore beetle and the cigarette beetle, both belonging to the family Anobiidae and have similar morphological characteristics and sizes. The former species exhibited 40% mortality, the latter 20%. It was apparent that cigarette beetles and drugstore beetles had about the same number of hastisetae on their bodies. It is speculated that the difference in mortality after 72 hr exposure was caused by the difference in their behavioral reaction to the hastisetal entanglement. Drugstore beetles actively cleaned off the hastisetae on their appendages and struggled to free themselves from the entanglement, whereas cigarette beetles did not appear to carry out cleaning behavior and remained quiet despite the hastisetae attached to their bodies. Since cigarette beetles did not spend much energy on cleaning behavior, they probably were less exhausted than drugstore beetles, resulting in lower mortality in the former species.

Nutting and Spangler (1969) placed some T. variabile larvae in a feeding chamber of several species of ants maintained in the laboratory. Workers of Pheidole sciophila that touched the Trogoderma larvae picked up the hastisetae and began cleaning movements. They stated that those ants unable to free themselves usually died after several hours of struggling, probably from exhaustion and dehydration.

Morphological factors that seemed to play important roles in the reaction of the stored-product beetles are:

(1) Body size (weight and strength)

(2) Setae on body (length, diameter, shape, numbers)

It is assumed and is consistent with the results that larger insects have more strength to get rid of attached hastisetae, and to free themselves when attached to other insects by the hastisetae. Extreme small size may be an advantage, as for booklice. Although they "picked up" loose hastisetae from the bottom of the boxes and became entangled, they appeared to be too light to become attached to, or pull off the hastisetae when they climbed on the Trogoderma larvae. Also booklice are quite fast moving and can walk backward when necessary. Nutting and Spangler (1969) mentioned the relative resistability of a bethylid parasite of Trogoderma larvae. The wasps mounted the larvae for oviposition but even when they walked over the larvae, they rarely detached more than a few hastisetae and never became entangled. They speculated that the wasps escaped serious entanglement because of their small size and lightness of touch, coupled with their agility to avoid the "striking" of the Trogoderma larvae.

The cadelle is one of the largest and strongest among stored-product insects. They successfully avoided hastisetal entanglement. This was also true for the two flour beetle species. Their strong mouthparts were very effective in cutting the hastisetae.

Another factor affecting susceptibility is the setae on the bodies of the insects. Their size, shape, and density seem to be important. Setae which are thick did not wedge deeply into the slots of the hastisetae and were temporarily attached, if at all. This is illustrated in Plate XVII, Fig. 2, for sawtoothed grain beetles. The hastisetae

were eventually pulled off by the beetle's cleaning behavior and thus mortality observed was relatively low. As shown in Plate XIII, Figs. 2 and 3, peculiar-shaped setae on the rice weevil body were quite susceptible to the hastisetal attachment. It seems reasonable that the more complex the structure of the setae, i.e., the more branched the setae, the more susceptible they are to hastisetal attachment. This was true for the shiny spider beetle. More hastisetae were found attached to their antennae (Plate XVIII, Fig. 2) and legs than to elytra, and it is probably due to shape of the setae.

Another factor that is probably important is the number of setae per unit area on the insects' bodies. The setae of the red flour beetle are sparse (Plate XI, Figs. 1 and 2), as were those of the lesser grain borer head area (Plate XVI, Fig. 3). The shiny spider beetle has very few hairs on the elytra, almost invisible to the naked eye, and the elytra are so smooth and shiny that it is unlikely that the hastisetae will attach (Plate XVIII, Figs. 3 and 4).

It is hypothesized that the following contribute to susceptibility of adult insects to hastisetal attachment:

(1) relatively small size (not strong enough to remove and escape from the hastisetal entanglement)

(2) active, thus more likely to contact Trogoderma larva or pick up loose hastisetae from the habitat, and to become weakened by continual attempts to escape.

(3) relatively thin or branched setae.

(4) high density of setae per unit area.

III. Ability of Two Species of Stored-Product Insects to Survive and Maintain Populations in the Same Culture with Trogoderma variabile.

Results of encounters of stored-product insects with Trogoderma larvae were described earlier. It seemed appropriate to examine the maintenance of a population by stored-product insect species in the same laboratory culture habitat with Trogoderma variabile larvae.

Mills and Partida (1976) showed that flat grain beetles, Cryptolestes pusillus (Schonherr) were easily and permanently entangled with Trogoderma hastisetae when confined in a small plastic box with a Trogoderma larva. They also stated that confused flour beetles, Tribolium confusum Jacquelin duVal were apparently strong enough to shed the hastisetae and avoided permanent entanglement in the same confined situation.

The results obtained in Experimental Test II indicated that of those insects tested, flat grain beetles were one of the most susceptible to entanglement by Trogoderma hastisetae, as shown by their high mortality, whereas very low or no mortality of confused or red flour beetles occurred. Experiments were designed to determine the differences between red flour beetles or flat grain beetles in ability to maintain their populations in the same habitat with T. variabile larvae.

The objectives of the experiments were; (1) to discern any effect of Trogoderma larvae on the parental population of the test insect species, and (2) to evaluate the accumulating effect of Trogoderma larvae through progeny populations of the test insects.

Materials and Methods

The number of insects introduced into each babyfood jar that had a volume of 160 cc was arbitrarily determined. As sexual dimorphism of the flat grain beetles is obvious, 10 males and 10 females were randomly chosen and put into each jar. The 20 red flour beetles in each jar were not sexed. The food medium was mixed according to the species in the jars and the medium was filled to about 75% of the jar (120 cc).

Trogoderma variabile vs. Flat grain beetle, Cryptolestes pusillus

Adult flat grain beetles were removed from two active culture jars and then discarded, leaving only immature stages in the medium. The culture jars were returned to the rearing room for 10 days, at which time emerged adults were sieved out and transferred to fresh medium for 6 days, thus the approximate age of the test insects was known (6 to 16 days), and they were mature. The food medium for the test was a 1:1 weight mixture of the flat grain beetle medium and T. variabile rearing medium described earlier. Twenty-four grams (120 cc in volume) of the mixed medium were provided in each babyfood jar. The inside walls around the mouth of the jars were coated with "teflon" to prevent the escape of the insects. Ten male and 10 female flat grain beetles were put into each jar. The jars were divided into 4 groups, a number of full-grown larvae (approximately the same size) of T. variabile was introduced into each jar. The number used in each babyfood jar in each group was 0 (as control group), 5, 15, or 25. Six replicates of each larval density were made. The mouth of each jar was covered tightly with nylon cloth held by a rubber band to prevent entrance of other insects. All jars were placed in the rearing room (27 $\pm$ 1°C, 67 $\pm$ 3%RH, 14:10; light:dark) until observation dates (at 25 and 75 days).

For the 25-day observation, 3 replicates of the test jars and 3 of controls were analyzed for live adult flat grain beetles and live T. variabile larvae and then discarded. At 75 days the remaining replicates were placed in a freezer (ca. -15°C) to kill all insects. Because of the large numbers of flat grain beetles after 75 days, each of the frozen samples was spread evenly in a pan and then divided equally into 4 parts. Only flat grain beetle adults in one of the parts were counted and an estimate was calculated for the total sample. The Trogoderma larvae in the entire sample were also counted.

Trogoderma variabile vs. red flour beetle, Tribolium castaneum

Procedures were the same as used in the preceding experiment except:

(a) Food medium was a 1:1 mixture of T. variabile medium and the red flour beetle medium.

(b) Twenty unsexed adult red flour beetles (age 10 to 16 days) were randomly selected and put into each jar together with the appropriate number of T. variabile larvae (0, 5, 15, or 25 per each jar).

(c) Observations were made at 30 and 90 days after the introduction of the insects. The dates were based on the longer developmental period of this species.

(d) Progeny counts of the red flour beetles on the observation dates were limited to adults. Both larvae and adults of T. variabile were counted. On the second observation date, adults in each entire sample were counted.

Results and Discussion

As the minimum developmental period of flat grain beetles is 25 days, at the first observation (25 days after introduction), all the live adults in the test jars were of the parental generation. On the second observation data (75th day), it was assumed that the adults in the jars were of the parent, F_1 and of F_2 generations.

Currie (1967) reported that the longevity of the flat grain beetle was 21.7 (3.7 - 30.7) weeks for males and 22.5 (14.1 - 26.8) weeks for females, reared at 25°C, 90%RH. At 27.5°C, 90%RH, it was 27.6 (24.0 - 32.1) weeks for males and 19.6 (6.7 - 30.3) weeks for females. Under my experimental conditions it takes a minimum of 30 days for the red flour beetle to complete development from egg deposition to adult emergence. Therefore at 30 days, it was expected that all the adult beetles present were of the parent generation. On the 90th day, adult beetles in the jars were of the parent, F_1 and perhaps F_2 generations. Longevity of the species is quite long. Good (1936) reported averages of 547 and 226 days for males and females, respectively, at 27°C. Most of the Trogoderma remained as larvae; except only one female adult Trogoderma was found in a replicate of the red flour beetle test, therefore it was unlikely that fertile eggs were laid. A possible explanation for lack of Trogoderma pupation in the jars is that all the larvae were females (the larvae used in this experiment were of similar size and the largest in the cultures; full-grown male larvae are much smaller than female) and may not pupate except when males are present. Beck (1971a) reported that some T. glabrum

larvae did not pupate as early or as frequently if adults of opposite sex were not present. Beck also stated that there seemed to be a critical period after which pupation would occur regardless of whether the other sex is present. This might explain the female adult found in one replicate. Results are shown in Table 2. As there was no reproduction of the Trogoderma species, their numbers were not included in the table. In most of the replications all Trogoderma larvae were found, but a few were dead. Cast-off skins on top of the media in some jars indicated larval molting.

At the first observation there were no significant differences between controls and test replicates in numbers of live adults for either species. An average of 19.7 parent red flour beetles were found in controls and 16.7 were found in the replicates originally with 25 Trogoderma larvae; these averages were not significantly different ($P<0.05$). At the second observation, the numbers of the insects found in the jars ranged from 1003 to 1539 per replicate, still not significantly different from controls ($P<0.05$).

An average of 19.0 parent flat grain beetles were found in controls and 17.3 in replicates originally with 25 Trogoderma larvae at the first observation. At the second observation, (75), however, the average number of flat grain beetles in the replicates with 25 Trodogerma larvae was significantly lower than the controls or the replicates with lower initial Trogoderma densities ($P<0.05$). The number of adult beetles ranged from 2284 to 2700 averaging 2549.3 in this group, while the other 3 treatments, i.e., Trogoderma larvae originally introduced at 0, 5, 15 per

Table 2. No. of flat grain beetle and red flour beetle adults after rearing with T. variabile larvae (original nos.: 10♂♂ & 10♀♀ for flat grain beetle or 20 randomly-selected red flour beetles per replicate).

No. of Trogoderma larvae placed in each replicate	After 30 days		After 90 days	
	Mean	Range	Mean[1/]	Range
	Red Flour Beetle			
0	19.7	19-20	1355.7a	1031-1332
5	19.7	18-21	1185.3a	1055-1403
15	16.7	11-20	1280.3a	1208-1388
25	16.7	19-21	1280.3a	1003-1539
	Flat Grain Beetle			
	After 25 days		After 75 days	
	Mean	Range	Mean[1/]	Range
0	19.0	18-20	4174.7a	3636-4552
5	18.0	17-19	3384.0a	3124-3800
15	19.3	18-20	4137.3a	3764-4816
25	17.3	16-19	2549.3b	2284-2700

1/ Means followed by the same letter are not significantly different at the 5% level (Duncan's multiple range test).

jar, averaged 4174.7, 3384.0, and 4137.3, respectively. Although the data indicated that the greater density of Trogoderma significantly inhibited flat grain beetle population, they did not prove that the Trogoderma hastisetae were the cause; however, Experimental Test II demonstrated that flat grain beetles were very susceptible to the hastisetae (see Table 1). Moreover, while the test jars were held in the rearing room until the observation dates, I twice observed adult flat grain beetles in the jars of the highest Trogoderma density apparently with their antennae bound together by hastisetae, and walking unnaturally, probably due to hastisetal attachments to their legs. The Trogoderma larvae continued to molt as larvae, leaving many cast skins on top of the medium. Any hastisetae not already "pulled" off the larvae are shed with cast skins, thus the total number of hastisetae in the jars increased with each larval molt. More flat grain beetles in the replicates with the highest Trogoderma density (25/rep.) were observed in the medium (not on top of it), as compared with those in the replicates with lower Trogoderma densities. This behavior may have been the avoidance of the larger quantity of cast skins and hastisetae on the surface. Therefore, it is probable that hastisetae were involved in suppression of the beetle population. More extensive studies using more densities of Trogoderma larvae should be conducted, and more frequent observations should be made of the test insects to better monitor the extent of hastisetal entanglement.

IV. Development of Fed T. variabile; Molting, Size, and Hastisetal Tufts.

Loschiavo (1960) studied the life-history and behavior of T. parabile (T. variabile). He described morphological changes of the larvae during development. My experiment was a similar study on larval growth, using Loschiavo's description as a guide.

Materials and Methods

Black construction paper was fitted to the bottom part of a petri dish (9-cm diam) and a stack of black paper squares (3 x 3 cm) was used for oviposition sites for T. variabile adults. Adults were aspirated from culture jars and introduced into the petri dish. No food was supplied, but a small amount of water was provided by placing 2 small pieces of water-soaked tissue paper in the petri dish. After 12 days, 40 first larval instar were removed from the petri dish by using a fine camel hair brush. Incubation period for the eggs ranged from 9 to 10 days; thus the ages of the larvae used for the experiment were 1 to 3 days old. The larvae were then put into #00 gelatin capsules, individually, with a small amount of food medium and placed in the growth chamber described earlier ($27 \pm 1°C$, 43%RH avg.). Daily observations were made of each capsule and an adequate amount of food was added. Five to 7 days after the molt, the size of the larva (body length and head capsule width) and the number of major hastisetal tufts was recorded. The larva was placed ventral side up for body length and head capsule width measurements because when observed dorsally, the body setae obscured the tip of the abdomen and the

base of the head. The major hastisetal tufts were arbitrarily defined as those tufts having abundant hastisetae when compared to the ones on other segments. Plate II, Fig. 2 shows 4 of the major hastisetal tufts seen laterally. Normally, full-grown larvae of the species have 4 pairs of the major hastisetal tufts on the 5th to 8th abdominal tergites.

Results and Discussion

Of 40 first instar larvae, 14 survived and became 7th instars. The data in Table 3 included only those 14 larvae.

Table 3. Mean duration of each developmental stadium (in days).

Stadium	Mean[1/]	Range
I	8.07 a	5.0 - 12.0
II	10.80 b	9.0 - 14.0
III	10.07 b	9.0 - 14.0
IV	10.29 b	9.0 - 12.0
V	10.46 b	9.0 - 20.0
VI	10.50 b	9.0 - 15.0
VII	12.64 c	9.0 - 15.0

1/ Means followed by the same letter are not significantly different at the 5% level (Duncan's multiple range test).

The durations of the first larval stadium were estimated, because exact ages of newly-hatched larvae were not known (see methods). Estimated duration for the first stadium was significantly shorter than the rest, 8.07 days, while the 7th stadium was the longest, 12.6 days. Mean durations of the other stadia were about 10 days and no significant differences were observed among them ($P<0.05$). According to Partida and Strong (1975), male T. variabile larvae took 48.4 days and female larvae 50.3 days from egg hatch to mature adult at 26.7°C and 50%RH. Although RH was less constant than theirs, under approximately the same conditions (27 ± 1°C, 43%RH avg.), the larvae in my test averaged of 60.5 days to become 6th instars. The larvae continued to molt without pupation until the 78th day, when the test was terminated because it was evident that pupation had been abnormally delayed by various factors (to be discussed later).

During the 78 days, 14 larvae molted 6 times and 7 molted 7 times. No sexual difference in larval stadia was determined. Partida and Strong (1975) reported that female T. variabile larvae usually molted once more than male larvae before pupation, i.e., females usually had 6 molts and males 5, if grown under optimum conditions. They stated that number of molts of each sex varied widely (4 to 9). Although there is a required minimum number of molts before pupation under certain environmental conditions, temperature and humidity changes may cause an increased number of molts (Partida and Strong, 1975).

Measurement of the larval dimensions was made 5 to 7 days after each molt, because it gave the larvae enough time to grow to approximately stable

size within the particular instar. Loschiavo (1960) reported dimensions of developmental stages of T. variabile based on 10 individuals for each life stage. Eggs, 1st to 6th instar larvae, pupae, and adults (body length and head capsule width) were measured. The rearing conditions were 32°C, 70%RH. Measurements by Loschiavo are compared with my data in Table 4. My data on body lengths and head capsule widths were statistically analyzed later on in this discussion.

Table 4. Comparisons of dimensions of T. variabile larval instars (Loschiavo, 1960, and my data).

No. of instar	Body length (mm)		Head capsule width (mm)	
	Loschiavo's Mean + SE	Mine Mean + SD	Loschiavo's Mean + SE	Mine Mean + SD
I	0.92 ± 0.02	1.06 ± 0.04	0.21 ± 0.00	0.19 ± 0.03
II	1.56 ± 0.03	1.38 ± 0.03	0.26 ± 0.00	0.21 ± 0.00
III	1.54 ± 0.01	1.77 ± 0.14	0.36 ± 0.01	0.28 ± 0.00
IV	2.90 ± 0.05	2.45 ± 0.36	0.52 ± 0.01	0.37 ± 0.03
V	4.17 ± 0.08	2.98 ± 0.45	0.64 ± 0.00	0.43 ± 0.08
VI	4.89 ± 0.15	3.88 ± 0.91	0.75 ± 0.01	0.53 ± 0.14

Care must be taken in interpreting the differences between Loschiavo's data and mine; both body lengths and head capsule widths of Loschiavo's were greater. The larvae observed in my experiment showed slower growth than Loschiavo's. Several factors may have caused the differences, e.g., handling procedures and experimental conditions (Loschiavo: 32°C, 70%RH,

mine: 26.7°C, 43%RH). As expected head capsule width was less variable than body length. Loschiavo considered the head capsule width a more reliable means of differentiation between instars. Number of major hastisetal tufts was the most variable of the characteristics I observed (Plate XX). Determination of whether a hastisetal tufts was "major" or not was subjective and not considered accurate enough for differentiation between instars. Also the numbers often did not change from one instar to the next and individual variations within the same instar were observed.

Dyar (1890) proposed an empirical rule regarding the width of the larval insect head; that is, successive larval instars have a species specific rate of growth when the dimensions are measured, thus the amount of growth of the head capsule width at each molt is predictable. Head capsule is not subject to change within a stadium, making the dimension a reliable and convenient measurement to determine the particular instar. Wigglesworth (1972) referred to Dyar's rule and stated that when the number of the instar is plotted against the logarithm of some measurement, not only of head widths but also of various parts of the insect body, straight lines are obtained.

Data obtained in my experiment were analyzed by using logarithms (natural log:Log_e) of head capsule widths (Log_eHCW) in relation to the number of the instars. The same procedure was employed for body lengths (Log_eBL). Regression analyses of both dimensions showed agreement with linear models and no significant deviations were detected ($P<0.01$). Plate XXI shows the predicted lines for the dimensions. $\hat{Y} = -1.913 +$

Plate XX. Number of major hastisetal tufts (pairs) of T. variabile developing larvae in relation to number of instar. Data presented as the Mean ± S.D.

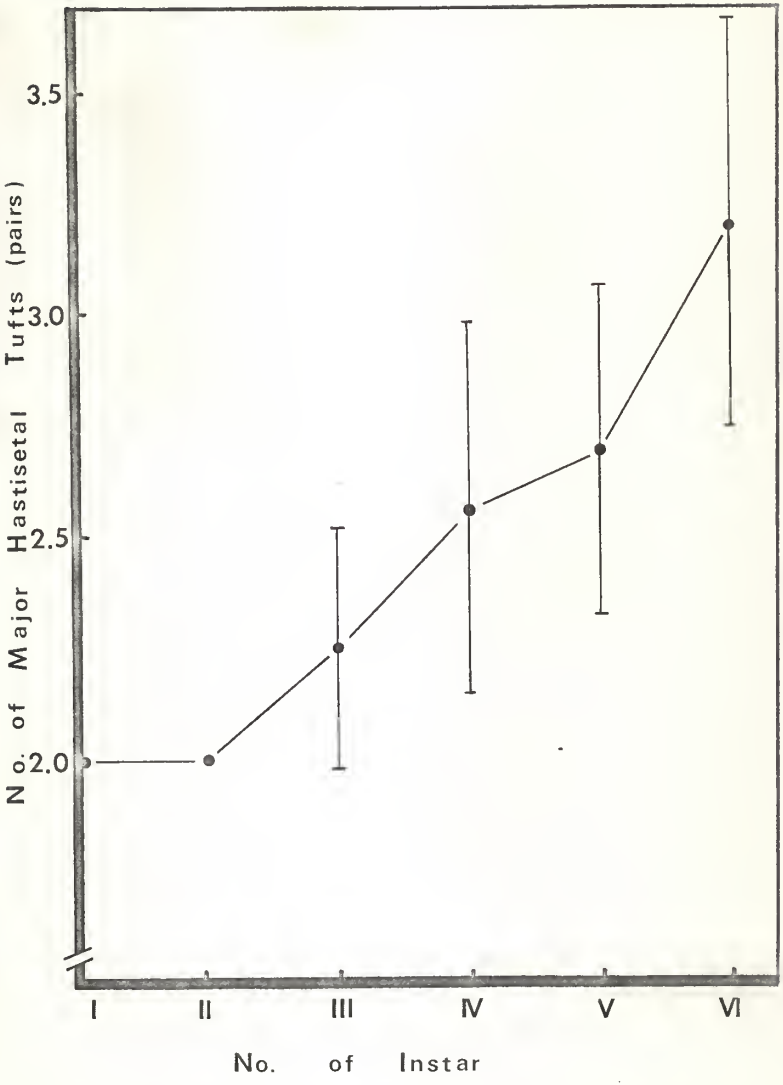
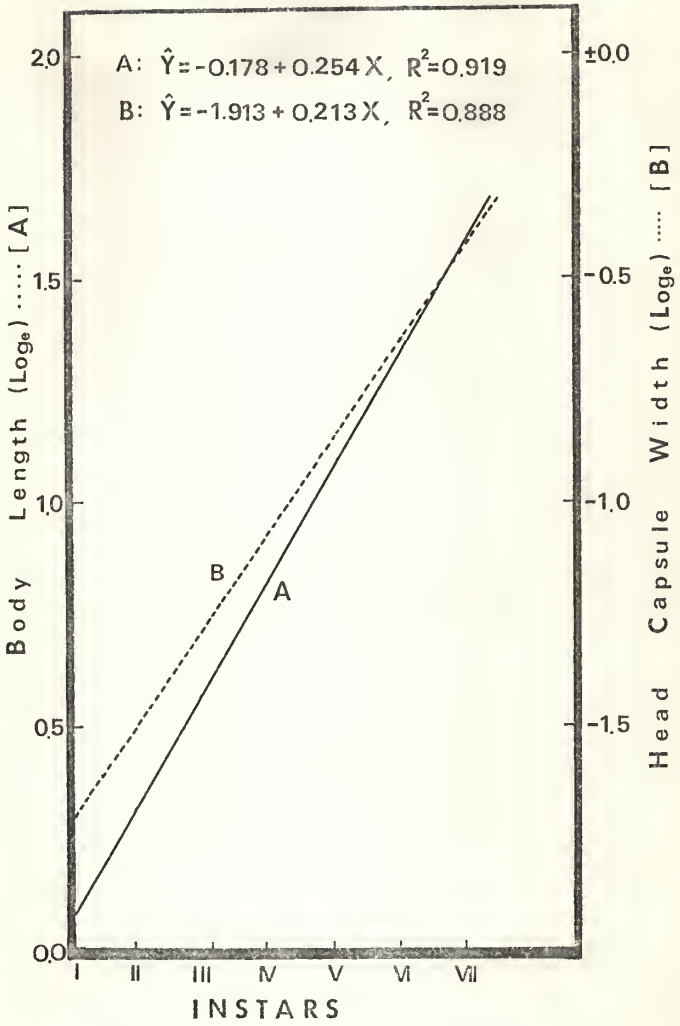

3.5
3.0
2.5
2.0
No. of Major Hastisetal Tufts (pairs)
I
II
III
IV
V
VI
No. of Instar

Plate XXI. Log_e-transformed body lengths [A] and head capsule widths [B] of T. variabile developing larvae in relation to number of instar.


A: $\hat{Y}$=-0.178+0.254X, R^2=0.919
B: $\hat{Y}$=-1.913+0.213X, R^2=0.888
Body Length (Loge) ..... [A]
Head Capsule Width (Loge) ..... [B]
2.0
1.5
1.0
0.5
0.0
±0.0
-0.5
-1.0
-1.5
B
A
I
II
III
IV
V
VI
VII
INSTARS

0.213X for Log_eHCW and $\hat{Y} = -0.178 + 0.254X$ for Log_eBL were obtained with R^2 values of 0.888 and 0.919, respectively, showing strong linear relationship between either Log_eHCW or Log_eBL and number of instars. Thus head capsule widths and body lengths of developing larvae followed Dyar's rule during the period of observation in the experiment. Richards (1949) pointed out that Dyar's rule holds only when durations of the stadia are of the same length. He showed that the longer the stadium, the greater the amount of growth, resulting in growth increase per unit of time being constant. The relationship will make a straight line if some dimension (absolute measurements) is plotted against accumulated developmental period. In some insects, the logarithm of the weights of successive instars plot on analogous straight lines, according to Richards. In my study, T. variabile larvae, especially from the 2nd to 6th instars, spent almost the same amount of time in each stadium (about 10 days). This is probably the reason the data fit Dyar's rule. However, Dyar's rule may be a special case of Richards' hypothesis, as various insects may have different lengths of developmental time in each stadium.

Loschiavo (1960) reported that T. variabile larvae normally molted 6 times before pupation but many fully-developed larvae did not become pupae after the 6th molt. These larvae continued to molt at irregular intervals without pupation. He compared larvae which had been treated in one of three different ways: A) handled and exposed daily to room temperature (21°-28°C), B) exposed daily for brief periods to room temperatures, C) undisturbed during the first 33 days of development. Sixty-eight percent of the larvae in category A, 67% in category B, and

32% in category C entered "diapause." These larvae remained as full-grown larvae for various periods; many of them molted 28 times in 11 months without becoming pupae. Referring to Loschiavo's observation, Burges (1961) stated that daily disturbance and handling was an important factor for "diapause" and also that small volumes of food and space delayed or inhibited pupation.

Beck (1971a) pointed out that the term "diapause" used by the earlier workers was actually a misnomer. In insects, diapause usually occurs at a pre-determined developmental stage and is triggered by such factors as seasonal temperature changes or changes in photoperiod. During the diapause, insects cease to feed and do not molt. Beck (1971a) showed that T. glabrum larvae, when conditions were not favorable for pupation, continued to feed and molt as larvae, even after gaining full size, resulting in "supernumerary larval instars." He also stated that if T. glabrum larvae "regrown" after starvation treatment, and subjected to an environment where additional dietary medium and a long-day photoperiod (16 hr) are provided, they consistently became "Dauer larvae" (Beck, 1972). Dauer larvae are nonpupating, maximum and stable-sized, and with supernumerary stadia. After becoming full-grown, T. glabrum female larvae, 1) metamorphosed into pupae, or 2) molted into additional supernumerary instars. Determining factors for pupation were: a) relatively high population density, b) sufficient rearing space, c) existence of a granular substrate, d) sufficient amount of food, e) existence of males of the species, and f) long-day photoperiod (Beck, 1971a). Apparently, the "diapause" larvae that Loschiavo (1960) referred to were Dauer larvae as described by Beck (1972).

It seems certain that the procedures employed in my experiment caused the larvae to become "supernumerary instars", thus delaying pupation, although T. variabile larvae increased their size at a consistent rate to 7th instars (Plate XXI). It is speculated that they would have become Dauer larvae if the experiment had continued, i.e. they would have neither pupated, nor increased their size. The following factors are probable causes of the "supernumerary larval instars" observed in my experiment:

a) handling disturbance: it was necessary to remove the larvae from the gelatin capsules to measure them after each molt, thus they were repeatedly handled and measured throughout the experiment.

b) small space: the larvae were held in #00 gelatin capsules.

c) individual rearing: the larvae were isolated, thus they were not exposed to the opposite sex, nor to a sufficient level of population density.

d) exposure to low temperatures: for more accurate measurement, each larva was placed in a refrigerator (10°C) for a few hours, then observed in a small petri dish which rested on an ice block for approximately 3 min. at each observation.

V. Effect of Starvation of Trogoderma variabile and Trogoderma inclusum on Their Molting, Size, and Hastisetal Tufts.

Riley (1883) first described long term starvation of Trogoderma tarsale, now believed to be T. inclusum. Wodsedalek (1917) reported an incidence of remarkably long starvation of the same species. Recently Beck (1971a, b, 1972, 1973a, b) extensively studied long term starvation of Trogoderma glabrum.

The objectives of my experiment were to investigate the effect of starvation on Trogoderma variabile and T. inclusum larvae and to determine changes of some characteristics that associate with starvation.

Materials and Methods

Thirty T. variabile full-grown larvae and 30 T. inclusum full-grown larvae were taken from each culture. Larvae of about the same size for each species were chosen and put individually into 1.5 x 5.5-mm glass vials without food. A cork stopper with a metal screen-covered hole was inserted in each vial. For convenience, the vials were then placed in holes in a styrofoam board (2.5 x 14.5 x 22.5 mm). The board with vials was then placed in the growth chamber described previously. Once a week, each vial was observed for an exuvia. When an exuvia was found, the vial was placed in a refrigerator at 10°C for a few hours to immobilize the larva prior to measurement. The immobilized larva was then placed in a glass petri dish (5 cm diam) which was resting on an ice block; this kept the

larva quiet for accurate measurement. The following measurements were made using an ocular micrometer in a binocular dissecting microscope: 1) body length, 2) head capsule width, and 3) number of major hastisetal tufts. The cast skin and fecal materials were removed from the vial and the vial was placed back in the chamber for future observations.

Results and Discussion

Trogoderma larvae do not eat their cast skins (exuviae) even when no food is available (Wodzedalek, 1917; Beck, 1971a). During the experiment, observations were made weekly. The larvae molted various times until termination of the experiment. All exuviae were intact, evidence that the larvae did not consume them. Weekly observations were terminated after 65 weeks for *T. variabile* and 35 weeks for *T. inclusum*.

Table 5 summarizes percent mortality and pupation at the final observation.

Table 5. Percent mortality and pupation at the end of each experiment for *T. variabile* and *T. inclusum*.

Trogoderma species	No. of insects observed	Observation period (in weeks)	% mortality	% pupation
T. variabile	30	65	43.3	3.3
T. inclusum	30	35	20.0	13.3

All cases of pupation occurred within 1 - 2 weeks after confinement of the larvae, and the adults emerged 1 - 2 weeks later; all were females. Unlike the T. glabrum studies by Beck (1971a), my procedure was not established to differentiate sexes of the larvae in accordance with culture age. It was assumed that the larvae exposed to starvation in my experiment were all females, as only larger larvae were selected for the test; female larvae are larger than males when fully grown. After 65 weeks of starvation, 58% of the T. variabile larvae were alive and after 35 weeks, 77% of T. inclusum larvae survived (Plate XXII). A few larvae apparently died during molting, for their exuviae were not completely cast off. It is not known how long the surviving larvae of both species would have lived beyond termination of the experiment. Thus in that regard, the data are incomplete. Riley (1883) found as many as 43 cast skins in a tight tin box in which two T. tarsale (T. inclusum) larvae were confined for 3.5 years without food.

During the observation period, the intervals between retromolts varied greatly. Plate XXIII shows average number of weeks between molts for the two species. T. variabile larvae averaged 1.52 $\pm$ 0.51 (mean $\pm$ S.D.) weeks before the first retromolt; T. inclusum, 2.50 $\pm$ 1.53 weeks. The former species spent 13.08 $\pm$ 9.67 weeks between the 3rd and 4th molts; the latter species, 7.68 $\pm$ 5.01 weeks; the longest intervals observed for the two species. Beck (1971a) reported that full-grown female larvae of T. glabrum usually underwent the initial retrogressive larval molts within 6 - 14 days after isolation. He also stated that the temporal pattern of retromolts seemed to be random.

Plate XXII. Survivorship of retrogressive Trogoderma larvae. Individuals that pupated (all within 2 weeks) were not included in calculations. T. variabile observations were terminated at 65 weeks; T. inclusum, at 35 weeks.

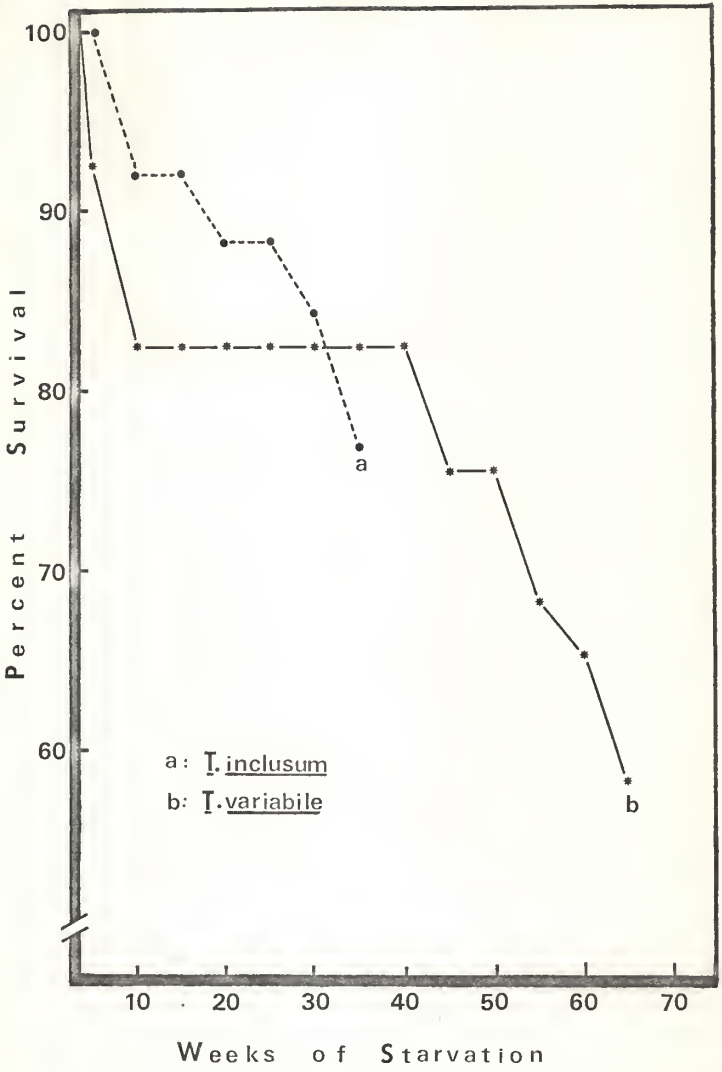
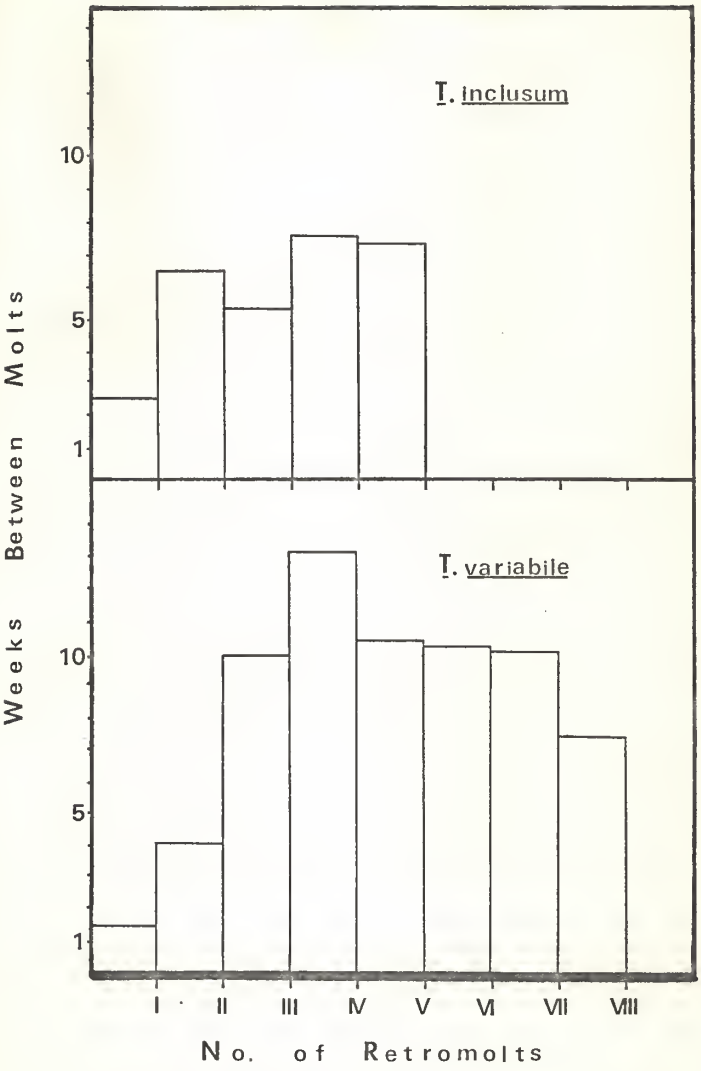

100
90
80
70
60
Percent Survival
a
b
a: T. inclusum
b: T. variabile
10
20
30
40
50
60
70
Weeks of Starvation

Plate XXIII. No. of weeks between successive retromolts.


T. inclusum
T. variabile
10
5
1
10
5
1
Weeks Between Molts
I
II
III
IV
V
VI
VII
VIII
No. of Retromolts

The relationship between accumulated number of molts and accumulated number of weeks of each individual, defined as "frequency of molts" by Beck (1972), was analyzed. Regression analyses between the two characteristics and the number of retrogressive molts observed in my experiment indicated good agreement with linear models and no significant deviations from linearity were detected ($P<0.01$). Table 6 shows regression coefficients (b: slopes of the regression lines), R^2 values (goodness of fit of the data to the predicted lines), and regression equations for the predicted lines. Data obtained in Experimental Test IV (fed T. variabile larvae) were treated in the same manner and included in the table for comparison.

Table 6. Relationship between no. of accumulated weeks and no. of accumulated molts (retrogressive for starved larvae): regression coefficients, R^2 values, and predicted linear regression lines.

Trogoderma species	b	R^2 value	Equation
T. variabile (starved)	0.104	0.820	$\hat{Y} = 1.036 + 0.104X$
T. inclusum (starved)	0.174	0.654	$\hat{Y} = 0.044 + 0.174X$
T. variabile (fed)	0.654	0.920	$\hat{Y} = 0.076 + 0.654X$

All three predicted lines showed high goodness of fit to the data. Beck (1972) found that the "frequency of molts" among T. glabrum female larvae varied according to the conditions under which the larvae were maintained. Progressive larvae (reared normally throughout the developmental period until pupation); stabilized larvae, or "Dauer larvae" (non-pupating larvae of maximum stable size); and retrogressive larvae (isolated individually without food) were analyzed for their frequency of molts. Progressive larvae exhibited the highest frequency (slope of regression = 1.298); retrogressive larvae, the lowest (slope of regression = 0.111); while Dauer larvae displayed an intermediate frequency of ecdysis (slope of regression = 0.434).

My data agreed with Beck's observations (1972). The slopes of the predicted linear regression lines (b) were 0.104 for retrogressive T. variabile larvae and 0.174 for those of T. inclusum. The slope of the regression line of developing (fed) T. variabile larvae (b = 0.625) was 3.5 to 6 times steeper than that of retrogressive larvae. The results are summarized in Plate XXIV together with Beck's observation for comparison. It is obvious that retrogressive larvae molted less frequently than developing larvae.

Table 7 shows the decreasing body lengths, head capsule widths, and the number of major hastisetal tufts, in relation to the number of retromolts.

Under starvation, T. variabile larvae significantly decreased in body lengths from 6.21 to 4.33 mm, in head capsule widths from 0.84 to 0.64 mm, and in number of major hastisetal tufts from 4.0 to 2.7 pairs. Significant decreases were also observed for T. inclusum larvae: body lengths from 5.36

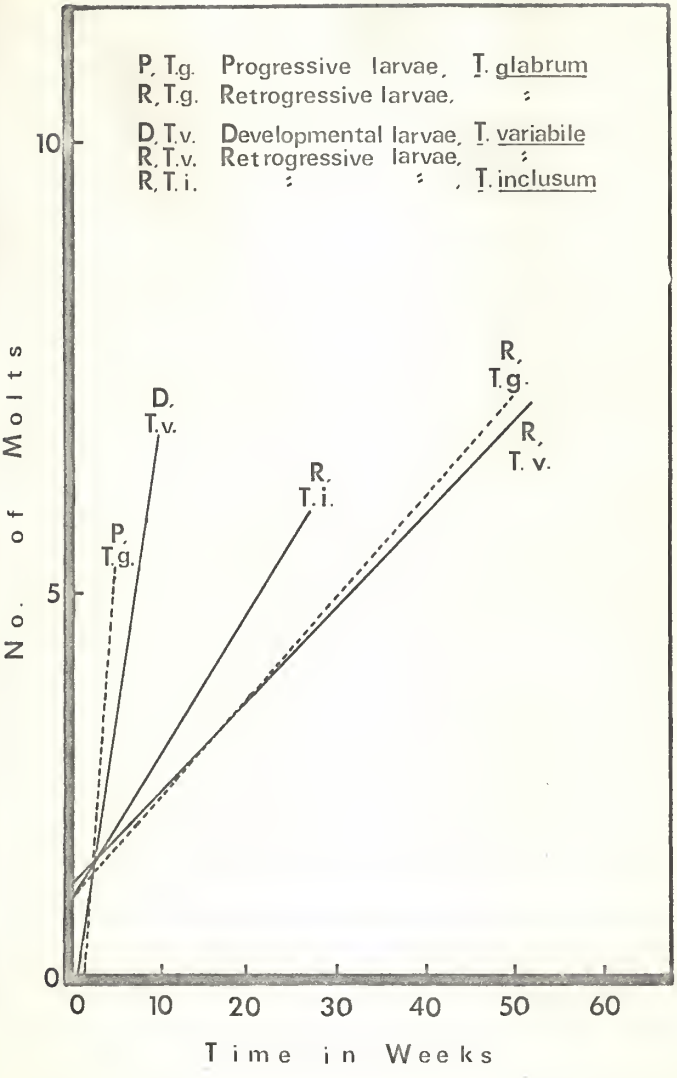
Table 7. Means of body lengths, head capsule widths and no. of major hastisetal tufts after successive retromolts.[1/]

No. of retromolts	larvae observed	Body length + S.D. (mm)	Head capsule width + S.D. (mm)	No. of major hastisetal tufts
		T. variabile		
0[2/]	16	6.21±0.35a	0.84±0.05a	4.00±0.00a
1	16	6.10±0.48a	0.82±0.08a	4.00±0.00a
2	16	5.91±0.46a	0.82±0.09a	3.84±0.24a
3	14	5.48±0.56b	0.80±0.08a	3.50±0.39b
4	16	5.18±0.48b	0.74±0.07b	3.22±0.41c
5	16	4.74±0.59c	0.70±0.08bc	2.94±0.36d
6	9	4.55±0.76c	0.67±0.07cd	3.00±0.43cd
7	5	4.33±0.93c	0.64±0.08cd	2.70±0.67d
		T. inclusum		
0[2/]	20	5.36±0.35a	0.86±0.06a	3.75±0.55a
1	20	5.16±0.38a	0.80±0.07b	3.73±0.30a
2	20	4.84±0.38b	0.73±0.07c	3.63±0.28ab
3	19	4.63±0.43bc	0.71±0.07d	3.56±0.25b
4	16	4.37±0.44c	0.65±0.06d	3.39±0.22b
5	6	4.19±0.57c	0.63±0.06d	3.42±0.42b

1/ Means followed by the same letters are not significantly different at the 5% level (Duncan's multiple range test).

2/ Larvae at the beginning of starvation (their original size).

Plate XXIV. Frequency of ecdysis among Trogoderma larvae. T. glabrum data were from Beck (1972).


P, T.g. Progressive larvae, T. glabrum
R, T.g. Retrogressive larvae, "
D, T.v. Developmental larvae, T. variabile
R, T.v. Retrogressive larvae, "
R, T.i. " " , T. inclusum
No. of Molts
10
5
0
D, T.v.
P, T.g.
R, T.i.
R, T.g.
R, T. v.
0
10
20
30
40
50
60
Time in Weeks

to 4.19 mm, head capsule widths from 0.86 to 0.63 mm, and number of major hastisetal tufts from 3.75 to 3.42 pairs. T. inclusum larvae were under observation for only 35 weeks while T. variabile larvae were observed for 65 weeks.

Plate XXV and XXVI show the decrease in the dimensions of retrogressive larvae expressed in percent of original size. After each retromolt, body lengths and head capsule widths of the two Trogoderma species larvae were compared with their original dimensions. After 7 retromolts, average T. variabile larval body length decreased to 69.04 $\pm$ 12.26% of its original length; head capsule width decreased to 75.54 $\pm$ 9.05% of original. After 5 retromolts, T. inclusum larvae decreased in body lengths to 79.63 $\pm$ 8.69% of original; head capsule widths to 74.88 $\pm$ 9.99% of original. Number of major hastisetal tufts also decreased as shown in Plate XXVII, however, as in the previous experimental test, variations of the data were very large.

As discussed in Experimental Test IV, developing T. variabile larvae showed consistent rates of growth for body lengths and head capsule widths in relation to the number of instars. The data were interpreted as a special case of Richards' (1949) hypothesis, fitting Dyar's rule because of similar lengths of successive larval stadia. The data obtained for the two species of retrogressive Trogoderma larvae were analyzed in similar manner. As shown in Plate XXIII, however, each species had variable lengths of molting intervals, suggesting that Dyar's rule would not fit. Thus regression analysis between body lengths or head capsule widths (both transformed into Log_e values) and the number of weeks of starvation were made according to Richards' hypothesis. The analysis agreed with linear

Plate XXV. Decrease of body lengths and head capsule widths of retrogressive T. variabile larvae (percent of original).

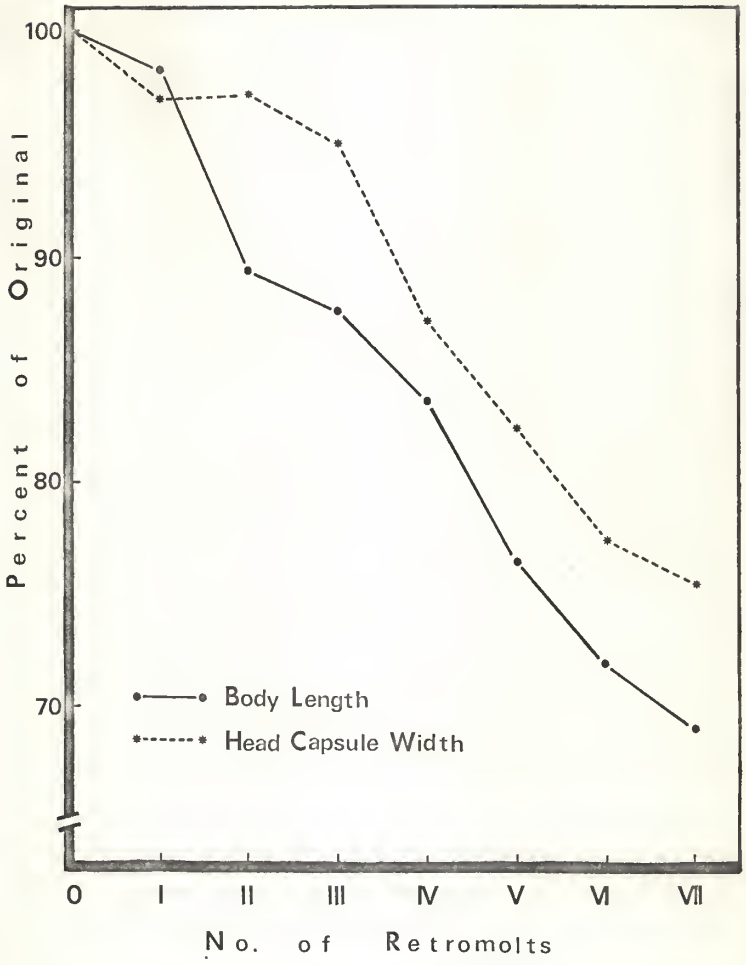

100
90
80
70
Percent of Original
Body Length
Head Capsule Width
0
I
II
III
IV
V
VI
VII
No. of Retromolts

Plate XXVI. Decrease of body lengths and head capsule widths of retrogressive T. inclusum larvae (percent of original).

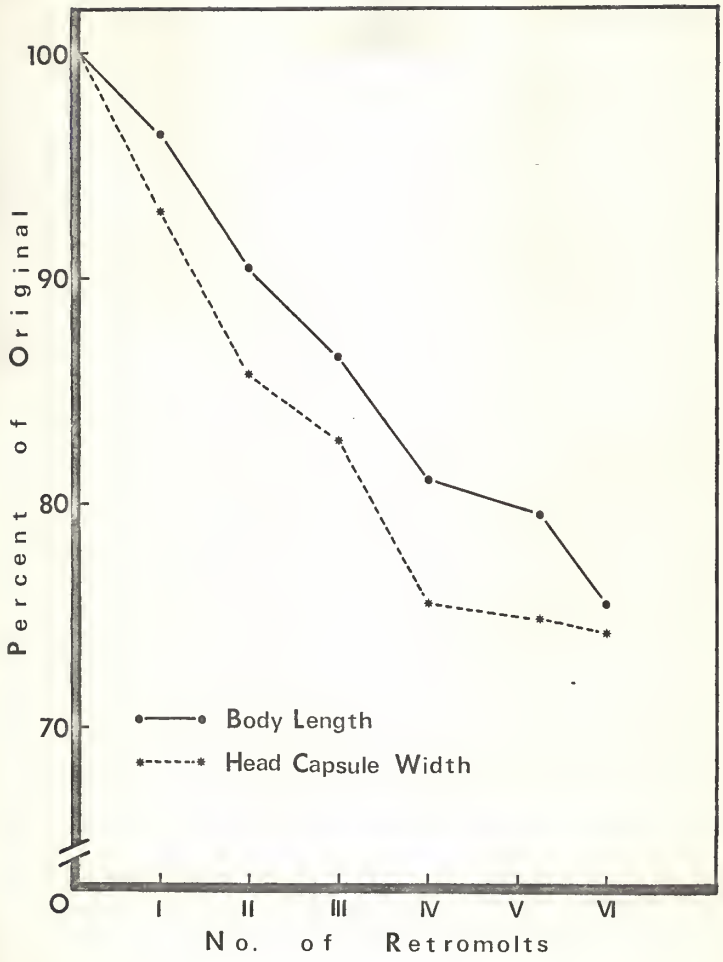
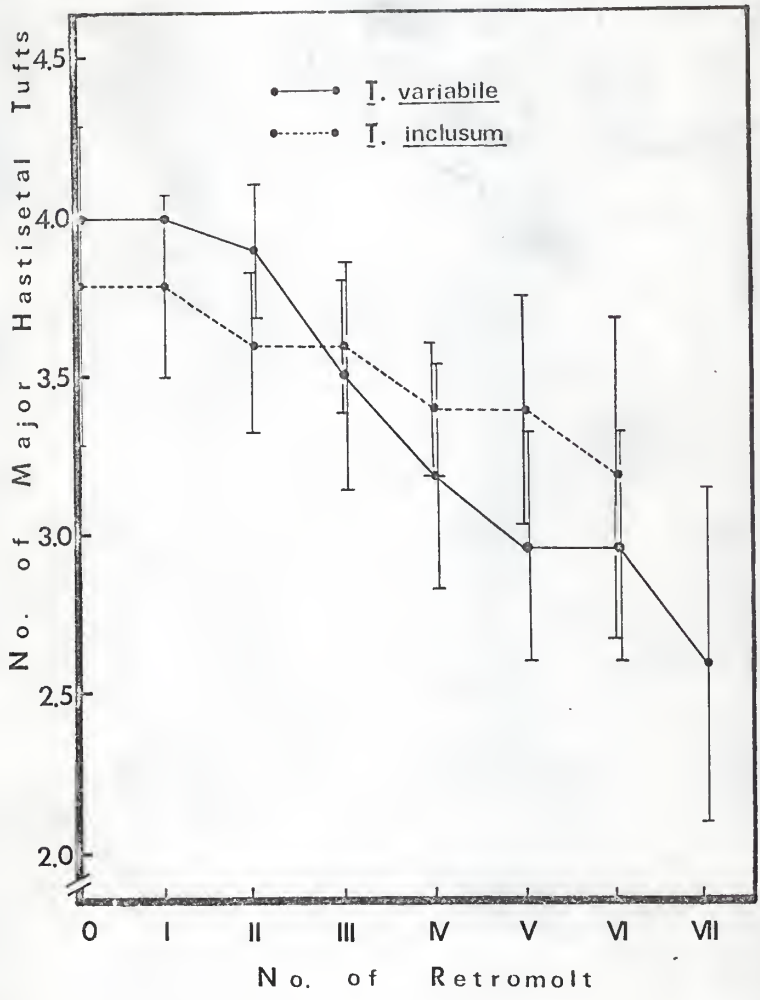

100
90
80
70
O
Percent of Original
Body Length
Head Capsule Width
I
II
III
IV
V
VI
No. of Retromolts

Plate XXVII. Decrease in number of pairs of major hastisetal tufts in relation to retromolts (bars indicate standard deviations; there was no variation for T. variabile prior to or after the lst retromolt).


T. variabile
T. inclusum
No. of Major Hastisetal Tufts
4.5
4.0
3.5
3.0
2.5
2.0
0
I
II
III
IV
V
VI
VII
No. of Retromolt

models and no significant deviations from linearity were detected. Plate XXVIII and XXIX show the relationship between these two dimensions and number of accumulated weeks for each species. Body lengths of T. variabile decreased at a greater rate than head capsule widths (Plate XXVIII), whereas the reverse was true for T. inclusum (Plate XXIX). Generally, T. inclusum larvae decreased in size more rapidly than T. variabile larvae, making the slopes of the regression lines of the latter species more steep than that of the former species. Accumulated effects of starvation, expressed in number of weeks in the abscissa of the two figures, were revealed in the proportionate decrease of body lengths and head capsule widths; i.e., when starved, both T. variabile and T. inclusum retrogressive larvae decreased their dimensions at consistent rates throughout the period observed, although R^2 values were not as high as those for the developing (fed) larvae discussed in experimental test IV.

Plate XXVIII. Relationship between Log_e-transformed body lengths [A] or head capsule widths [B] and no. of weeks of exposure to starvation (T. variabile).

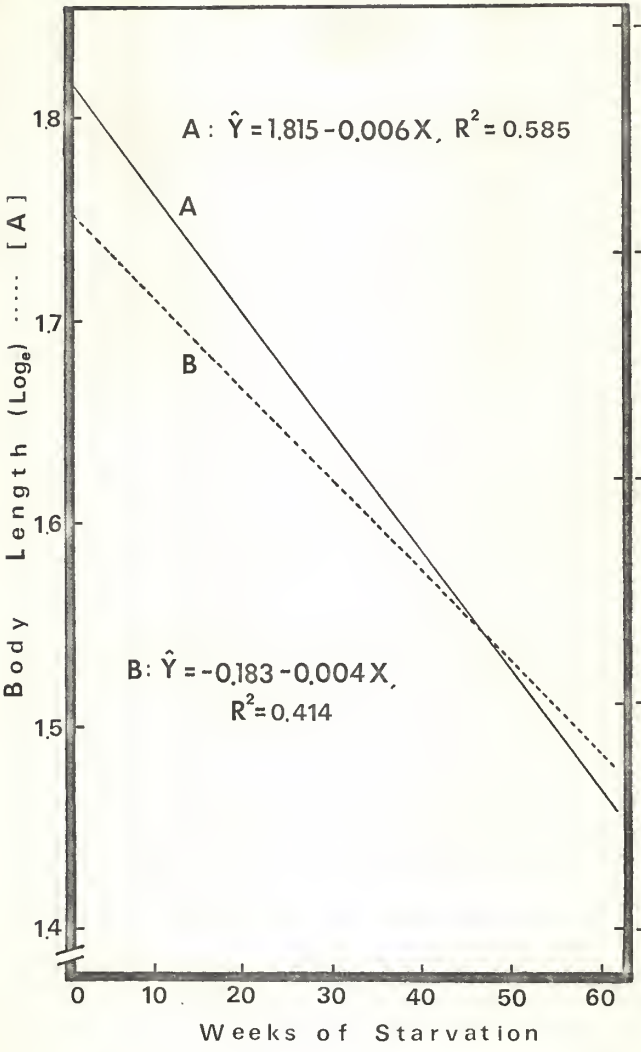
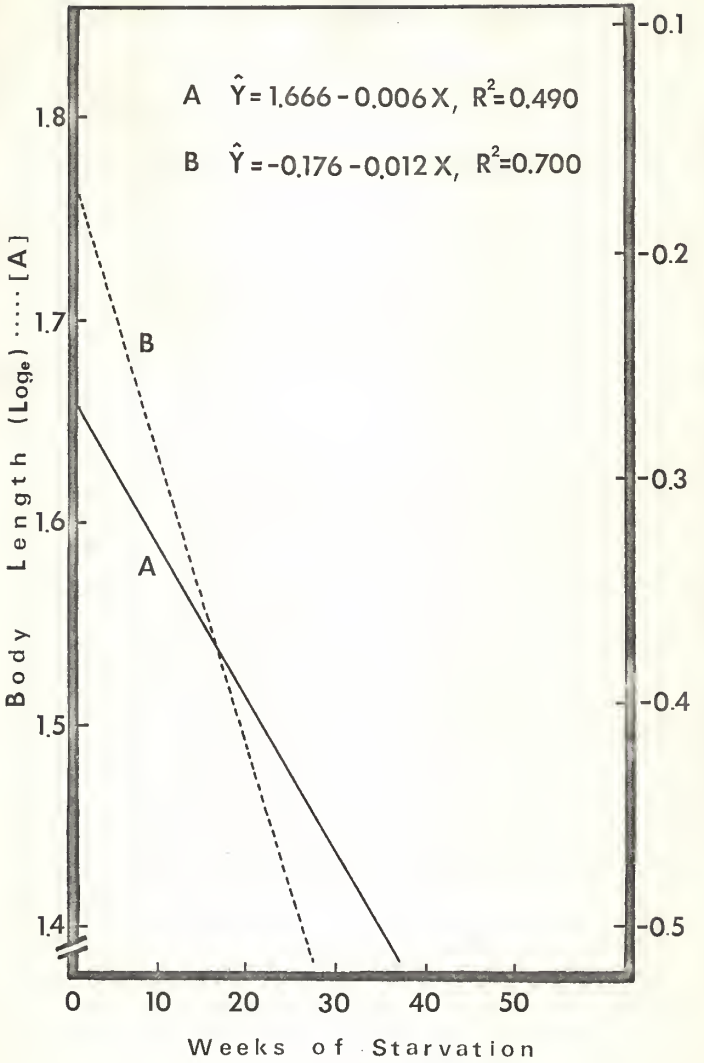

A : $\hat{Y} = 1.815 - 0.006X$, $R^2 = 0.585$
A
B
B: $\hat{Y} = -0.183 - 0.004X$,
$R^2 = 0.414$
Body Length (Log_e) ..... [A]
Head Capsule Width (Log_e) ..... [B]
1.8
1.7
1.6
1.5
1.4
-0.1
-0.2
-0.3
-0.4
-0.5
0
10
20
30
40
50
60
Weeks of Starvation

Plate XXIX. Relationship between Log_e-transfored body lengths [A] or head capsule widths [B] and no. of weeks of exposure to starvation (T. inclusum).


A $\hat{Y}$ = 1.666 - 0.006 X, R^2 = 0.490
B $\hat{Y}$ = -0.176 - 0.012 X, R^2 = 0.700
Body Length (Log_e) ..... [A]
Head Capsule Width (Log_e) ..... [B]
Weeks of Starvation
1.8
1.7
1.6
1.5
1.4
-0.1
-0.2
-0.3
-0.4
-0.5
0
10
20
30
40
50
A
B

CONCLUSIONS

Adult Trogoderma possess a degree of resistability to the potentially harmful larval hastisetae. None of the adult Trogoderma tested died during 72 hr exposure to their larvae, although the hastisetae did attach to parts of the adult body. Both male and female adults have cavities into which their antennae are retracted and protected from the hastisetae. Most of the setae on the Trogoderma adults were generally resistant to permanent hastisetal attachment because of their relatively large size. However the small setae found on the hindwings were very vulnerable to hastisetal attachment, although the hindwings were not usually exposed. The higher the density of the setae, the more prone to hastisetal attachment, as shown on the antennae. The behavior of the adults, such as efficient cleaning behavior using mouthparts and legs to rid themselves of the attached hastisetae, pupation on medium surface, and adults staying in the last larval skins until maturity, are mechanisms which probably offer protection from the larval hastisetae.

Relative susceptibility of 11 stored-product beetles to Trogoderma larval hastisetae was evaluated. Mortality of the adult insects after 72 hr revealed species specific responses to the hastisetae. The most susceptible species, thus having the highest mortality, were the rice weevil and the flat grain beetle; whereas the red flour beetle, the confused flour beetle, the shiny spider beetle, and cadelle were the least susceptible, showing very low or no mortality. The rest of the species were intermediate in susceptibility. Larvae of the flat grain beetle and those of the red flour beetle were also exposed to Trogoderma larvae

using the same procedure as for adults. The results showed that an average of 26.7% of flat grain beetle larvae died entangled by the hastisetae, whereas there was no mortality of the red flour beetle larvae. It was hypothesized that the differences in relative susceptibility of the insects against hastisetae were dependent on a) strength of the insect, b) degree of activity of the insect, and c) size, shape, and density of the setae on the insect.

Possible interspecific competition between Trogoderma larvae and the flat grain beetle or the red flour beetle in the same habitat was examined. There were no significant differences between parent population survival of either the flat grain beetle or the red flour beetle exposed to various numbers of Trogoderma larvae. However, after 3 generations (P, F_1, F_2) of the flat grain beetles that were exposed to the highest Trogoderma larval density, significantly lower population size was observed. There were no significant differences between progeny counts after emergence of the 3rd generation of the red flour beetle. Whether the suppression of the flat grain beetle population was caused by Trogoderma larval hastisetae is not known. Further studies are needed to determine whether other stored-product insect populations would be suppressed by Trogoderma, and to determine the mechanisms which cause it.

Observations of developing Trogoderma variabile larvae were made; duration of each larval stadium and linear measurements of the larvae were recorded. The head capsule widths and body lengths (transformed into Log_e-Values) increased at the same rates, following Dyar's rule, throughout the period observed. None of the larvae pupated during the observation period, which exceeded the "normal" developmental time, suggesting that

they became supernumerary instars. Factors, such as handling disturbance of the larvae, small rearing space, individual rearing, and exposure to low temperature, were considered as causes of delayed pupation.

Thirty full-grown T. variabile larvae were exposed to starvation for 65 weeks and 30 T. inclusum for 35 weeks. Larvae of both species showed strong resistance to starvation; 58% of T. variabile larvae and 77% of T. inclusum larvae were still alive after the respective starvation periods. The head capsule widths and body lengths of both species decreased at consistent rates during the period. The decrease of the dimensions followed Richards' hypothesis; log-transformed data on head capsule widths or body lengths in relation to accumulated number of weeks starved gave straight lines. In T. variabile, body lengths decreased faster than head capsule widths, whereas the reverse was the case in T. inclusum. Number of weeks between successive retromolts varied greatly; the first retromolts occurred 1.5 to 2.5 weeks after isolation, whereas the rest of the stadia tended to be longer. Molting frequency (number of molts in relation to number of weeks accumulated) of my data agreed with Beck's (1972); starved larvae molted less frequently than developing larvae.

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LITERATURE CITED

Bains, S. S. and A. S. Atwal. 1972. Protection of grain against Trogoderma granarium and Sitophilus oryzae. Bull. Grain Tech. 10: 213-217.

Bains, S. S., G. S. Battu, and A. S. Atwal. 1977. On the interspecific competition between Trogoderma granarium Everts and Sitophilus oryzae L., infesting stored wheat under different physical environments. Indian J. Ecol. 4: 75-84.

Beal, R. S., Jr. 1954. Biology and taxonomy of the Nearctic species of Trogoderma (Coleoptera:Dermestidae). Univ. of Calif. Pub. in Entomol. 10: 35-102.

Beal, R. S., Jr. 1956. Synopsis of the economic species of Trogoderma occurring in the United States with description of a new species (Coleoptera:Dermestidae). Ann. Entomol. Soc. Am. 49: 559-566.

Beal, R. S., Jr. 1960. Description, biology, and notes on the identification of some Trogoderma larvae (Coleoptera:Dermestidae). USDA Tech. Bull. 1228, 26pp.

Beck, S. D. 1971a. Growth and retrogression in larvae of Trogoderma glabrum (Coleoptera:Dermestidae). 1. Characteristics under feeding and starvation conditions. Ann. Entomol. Soc. Am. 64: 149-155.

Beck, S. D. 1971b. Growth and retrogression in larvae of Trogoderma glabrum (Coleoptera:Dermestidae). 2. Factors influencing pupation. Ibid. 64: 946-949.

Beck, S. D. 1972. Growth and retrogression in larvae of Trogoderma glabrum (Coleoptera:Dermestidae). 3. Ecdysis and form determination. Ibid. 65: 1319-1324.

Beck, S. D. 1973a. Growth and retrogression in larvae of Trogoderma glabrum (Coleoptera:Dermestidae). 4. Developmental characteristics and adaptive functions. Ibid. 66: 895-900.

Beck, S. D. 1973b. Crowth and retrogression in larvae of Trogoderma glabrum (Coleoptera:Dermestidae). 5. Effects of repeated retrogressions. Ibid. 66: 1051-1054.

Beck, S. D. and R. K. Bharadwaj. 1972. Reserved development and cellular aging in an insect. Science (Washington) 178: 1210-1211.

Burges, H. D. 1961. The effect of temperature, humidity and quantity of food on the development and diapause of Trogoderma parabile Beal. Bull. Entomol. Res. 51: 685-696.

Currie, J. E. 1967. Some effects of temperature and humidity on the rates of development, mortality and oviposition of Cryptolestes pusillus (Schonherr) (Coleoptera:Cucujidae). J. Stored Prod. Res. 3: 97-108.

Dyar, H. G. 1890. The number of molts of Lepidopterous larvae. Psyche 5: 420-422.

Elbert, Von A. 1976. Elektronenmikroskopische Untersuchungen der Pfeilhaare verschiedener Arten der Anthreninae (Col. Dermestidae). Anzeiger fur Schadlingskunde Pflanzenschutz Umweltschutz. 49: 81-83.

Good, N. E. 1936. The flour beetles of the genus Tribolium. USDA Tech. Bull. 498. 58 pp.

Hadaway, A. B. 1956. The biology of the dermestid beetles, Trogoderma granarium Everts and Trogoderma versicolor (Cruetz). Bull. Entomol. Res. 46: 781-796.

Hinton, H. E. 1945. A monograph of the beetles associated with stored products. Vol. 1. British Museum (Natural History) London, 443 pp.

Khare, B. P. 1965. Starvation resistance of some coleopterous insect pests of stored grain. Indian J. Entomol. 27: 489.

Kvenberg, J. E. 1978. Scanning electron microscopic study of adult stored product beetle elytra. J. Assoc. Official Analytical Chem. 61: 76-87.

Loschiavo, S. R. 1960. Life-history and behavior of Trogoderma parabile Beal (Coleoptera:Dermestidae). Can. Entomol. 92: 611-618.

Ma, M., W. B. Burkholder, and S. D. Carlson. 1978. Supra-anal organ: a defensive mechanism of the furniture carpet beetle, Anthrenus flavipes (Coleoptera:Dermestidae). Ann. Entomol. Soc. Am. 71: 718-723.

Mills, R. B. and G. J. Partida. 1976. Attachment mechanisms of Trogoderma hastisetae that make possible their defensive function. Ann. Entomol. Soc. Am. 69: 30-33.

Mroczkowski, M. 1968. Distribution of the Dermestidae (Coleoptera) of the world with a catalogue of all known species. Ann. Zoologici. 26: 16-191.

Nutting, W. L. and H. G. Spangler. 1969. The hastate setae of certain dermestid larvae: an entangling defense mechanism. Ann. Entomol. Soc. Am. 62: 763-769.

Okumura, G. T. 1967. A report of canthariasis and allergy caused by Trogoderma (Coleoptera:Dermestidae). California Vector Views, 14(3): 19-22.

Partida, G. J. and R. G. Strong. 1975. Comparative studies on the biologies of six species of Trogoderma: T. variabile. Ann. Entomol. Soc. Am. 68: 115-125.

Richards, O. W. 1949. The relation between measurements of the successive instars of insects. Proc. Royal Entomol. Soc. London. A, 24: 8-10.

Riley, C. V. 1883. Number of molts and length of larval life as influenced by food. American Naturalist. 17: 547-548.

Strong, R. G. 1975. Comparative studies on the biologies of six species of Trogoderma: T. inclusum. Ann. Entomol. Soc. Am. 68: 91-104.

Strong, R. G., G. T. Okumura, and D. E. Sbur. 1959. Distribution and host range of eight species of Trogoderma in California. J. Econ. Entomol. 52: 830-836.

Wigglesworth, V. B. 1972. The principles of insect physiology. (7th ed.) Methuen & Co., London, 827 pp.

Wodsedalek, J. E. 1917. Five years of starvation of larvae. Science (Washington) 46: 366-367.

Yinon, U. and A. Shulov. 1969. Bioassay of the response of Tribolium castaneum to repellent substance excreted by Trogoderma granarium. Ent. exp. and appl. 12: 191-205.

STUDIES OF *TROGODERMA* SPECIES DEVELOPMENT AND STARVATION, AND EFFECTS OF THEIR HASTISETAE ON SELECTED STORED-PRODUCT INSECTS

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This study was to determine the effects of larval Trogoderma hastisetae on thirteen selected stored-product insects, including Trogoderma adults, and to observe the attachment mechanisms of the hastisetae.

Five insects were placed together with 3 full-grown larvae of either T. variabile or T. inclusum in a small plastic box (3 replicates for each species and 3 controls with no Trogoderma larvae). Observations were made using a binocular microscope at 12, 24, 48, and 72 hr after introduction, and the insects were later used for scanning electron microscopy to further observe the attachment of hastisetae.

Adult Trogoderma resisted the entangling effects of the hastisetae, although their hindwings, when exposed, were vulnerable. Rice weevils, flat grain beetles, and foreign grain beetles were highly susceptible to the hastisetae; 70 - 100% of the beetles died entangled by the hastisetae within the 72-hr period. Drugstore beetles, sawtoothed grain beetles, lesser grain borers, and cigarette beetles were intermediate in susceptibility; 20 - 40% of the beetles were observed dead after 72 hr. Shiny spider beetles, red flour beetles, confused flour beetles, and cadelles exhibited very low or no mortality. Factors that may have influenced the relative susceptibility of the test insects were: 1) strength of the insects, 2) degree of activity, and 3) size, shape, and density of the setae on the insect's body.

Interspecific competition between T. variabile larvae and the flat grain beetles or red flour beetles was examined. At the first observation, when only parent populations were present, there were no

significant differences in the number of adult beetles in test jars in which 0, 5, 15, or 25 Trogoderma larvae were initially introduced. However, at the second observation, when jars contained P, F_1, and F_2 generations, there were significantly fewer flat grain beetles in the treatments with the highest Trogoderma larval density (25). No significant differences were found among the treatments for the red flour beetle populations. It is speculated that larval Trogoderma hastisetae were a factor in the cause of the flat grain beetle population suppression. Further investigation is needed to prove this hypothesis.

Studies were made of selected characteristics associated with Trogoderma development, under starvation and in the presence of food. Thirty T. variabile and 30 T. inclusum full-grown larvae were isolated in glass vials individually without food and observed weekly (T. variabile for 65 weeks; T. inclusum for 35 weeks). Body lengths, head capsule widths, and number of "major" hastisetal tufts were recorded after each retromolt. Log-transformed data on body lengths and head capsule widths in relation to the accumulated number of weeks starved resulted in straight lines and thus exemplified Richards' hypothesis (derived from Dyar's law). T. variabile provided with food became "supernumerary instars", probably due to handling of the insects and inactivating them by cooling for accurate linear measurements. The fed larvae molted more frequently than starved larvae, which agreed with Beck's (1972) report.